Ecole Doctorale GAIA (n°584)

Biodiversité, Agriculture, Alimentation, Environnement, terre, Eau

Mémoire présenté en vue d'obtenir

l'**Habilitation à Diriger des Recherches**

Sink regulation in rice as a way to explain contrasted performances of high-yielding genotypes

An approach to improve the efficiency of grain filling and of resources use under climate change constraints?

par

Tanguy Lafarge

Chercheur, Cirad, UMR AGAP

Adaptation et Amélioration Génétique et Adaptation des Plantes méditerranéennes et tropicales

Soutenue le 12 juin 2017 devant le jury d'examen:

Lydie GUILIONI, Maître de Conférences, SupAgro, Examinateur, Président du Jury

Alexandra JULLIEN, Professeur AgroParisTech, Rapporteur

Bruno ANDRIEU, Directeur de Recherches INRA Grignon, Rapporteur

Jacques Le GOUIS, Directeur de Recherches INRA Clermont, Rapporteur

Rachid SERRAJ, Directeur de Recherches, CGIAR Science Council, Examinateur

Tanguy LAFARGE, PhD, 46 years old
Senior Crop Physiologist, UMR AGAP, CIRAD, Montpellier, France

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Scientific expertise

Rice yield potential: ideotypes, whole-plant sink regulation, panicle architecture, hybrid rice
Adaptation to climate change: spikelet sterility, plant respiration, growth under water deficit
Crop physiology: organo-morphogenesis, gas exchange, source:sink and soluble sugar dynamics
Crop modeling: yield predictions under climate scenarios
Plant phenotyping: Genome Wide Association Studies (GWAS) and QTL mapping

Education

Ph.D. 1998, University Paris XI, Crop Physiology
M.Sc.1994, University Paris XI, Plant Ecophysiology
B.Sc. 1992, University Paris XI, Biochemistry and Molecular Biology

Professional positions held (since terminal degree)

- 03/2002 - present **Crop Physiologist**, Food Crop Program (2002-2005), UPR AIVA (2006-2010), UMR AGAP (2011-present), CIRAD, France
- 01/2011 - 12/2014 **Team Leader**, UMR AGAP, Cirad-BIOS, France
- 01/2011 - 12/2012 **Scientific Coordinator**, UMR AGAP, CIRAD-BIOS, France
- 04/2010 - 12/2010 **Team Leader**, UPR AIVA, CIRAD-BIOS, France
- 07/2008 - 04/2010 **Deputy Division Head**, CES Division, IRRI, Philippines
- 05/2007 - 12/2010 **Adjunct Professor**, Agronomist, UPLB, Philippines
- 03/2002 - 03/2010 **Scientist** then **Senior Scientist**, Crop Physiologist, IRRI, Philippines
- 09/1999 - 09/2001 **Assistant Professor**, Plant Physiologist, University Montpellier, France
- 09/1998 - 09/1999 **Postdoctoral Fellow**, Crop Physiologist, DPI, Australia

Major research activities and literature reviews (1994 - present)

2010-present (UMR AGAP, Cirad-BIOS, Montpellier, France)**: Senior Crop Physiologist**

- Copping rice with climate change:
  - Spikelet sterility under heat and high vapor pressure deficit: escape, avoidance and tolerance strategies, microclimate, leaf and panicle transpiration, time of the day of anthesis, phenotyping, Genome Wide Association Studies, QTL identification
  - Reduced yield and high night temperature: microclimate, maintenance and growth respiration, soluble sugar concentration, Q10 value and implications for crop models
  - Adaptation to transient soil water deficit: fraction of transpirable soil water, plant transpiration, leaf, internode and root elongation, shoot and root biomass partitioning, dissection for panicle initiation, phenotyping, Genome Wide Association Studies
  - Simulation of crop yield under future scenarios: simulation exercises of biomass and grain yield with the Samara crop model, model inter-comparison under AgMIP Initiative
- Increasing rice yield potential:

- Whole-plant regulation of panicle architecture: primary and secondary branch size and number and spikelet number, relative growth rate, tillering rate, soluble sugar concentration, near-isogenic lines, yield components and grain yield
- Traits for higher yield and superiority of hybrid rice: growing season and maturity group dependent relevant traits, crop phenology, sink regulation, organ vigor, biomass partitioning and harvest index, delayed leaf senescence, whole-plant architecture, yield components and grain yield

2005-2010 (CESD, IRRI, Los Baños, Philippines)**: Senior Crop Physiologist**

- Increasing rice yield potential: hybrid/inbred, seedling vigor, plant architecture (plant height, leaf angle, light interception), radiation use efficiency, biomass and leaf area production, sink regulation (tillering dynamics, root growth, culm elongation, panicle growth, leaf and culm vigor, grain filling dynamics), soluble sugar content, sink size, tiller and root senescence, yield components, grain yield
- Saving water in rice: water control, perched water table, soil and meristem temperature, soil and plant water potential, stomatal conductance, root distribution, fraction of transpirable soil water, shoot/root ratio, water productivity, yield components and grain yield
- Copping rice with climate change: elevated temperature and CO_2, vapor pressure deficit, staggered planting, leaf and panicle temperature, leaf and panicle transpiration, radiation use efficiency, crop phenology, leaf elongation rate, threshold temperature, sink regulation, soluble sugar content, leaf senescence, spikelet sterility, panicle architecture, yield components and grain yield

2002-2005 (CSWS, IRRI, Los Baños, Philippines)**: Crop Physiologist**

- Improving rice crop establishment: transplanting/broadcasting/row seeding, seed rate (direct seeding and nursery), seedling age at transplanting, planting density, leaf and tiller emergence, clump architecture (tiller angle) and plasticity, yield components and grain yield
- Increasing rice yield potential: hybrid/inbred, seedling vigor, plant architecture (plant height, leaf angle, light interception), radiation use efficiency, biomass and leaf area production, tillering dynamics, leaf vigor, sink size, tiller senescence, yield components, grain yield

1998-2001 (APSRU, DPI, Toowoomba, Queensland, Australia, and LEPSE, INRA, Montpellier, France)**: Crop Physiologist**

- Simulating sorghum leaf area production: micro-climate and thermal time, leaf emergence, tiller emergence and mortality, phyllochron, leaf area index and leaf area profile, organ biomass, specific leaf area, yield components, grain yield

1994-1998 (UR FPV, Cirad-CA, Montpellier, France, and IER, Bamako, Mali)**: PhD student**

- Simulating sorghum leaf area production: micro-climate and thermal time, leaf initiation and emergence, leaf, sheath and internode elongation, plastochron and phyllochron, leaf area index and leaf area profile

Leadership and Research Management

Team Leader (16 scientists), Phenotypic Plasticity and Adaptation of Monocots, UMR AGAP, CIRAD, 2010 - 2014

Scientific Coordinator (50 scientists), Development and Adaptation, UMR AGAP, CIRAD, 2011 - 2012

Deputy Division Head (25 scientists, 100 staff), Crop and Environmental Sciences Division, IRRI, 2008 - 2010

Symposium coordinator

Symposium **"Increasing yield potential: from physiological processes to ideotyping".** The 4th International Rice Congress, 27 Oct - 1 Nov 2014, BITEC, Bangkok, Thailand. IRC14-1192

Symposium "**Breeding for a 2030 world: some issues and opportunities**". Global Science Conference on Climate-Smart Agriculture, 24-26 October 2011, Ede-Wageningen, The Netherlands

Teaching Position

Adjunct Professor, Department of Agronomy, University of the Philippines Los Baños, 2006-2009

Assistant Professor, Plant Physiology Department, University Montpellier, France, 1999-2001

Private expertise and recent grants

Expertise for the improvement of the Breeding Program, Bayer Crop Science Company, 2013-present

RESPIRICE, Response of rice respiration to increase in night temperature: consequences for biomass and grain production and crop modeling / Bayer Crop Science / 2012-2014 / 126 k€

DRYCE, Idenification, validation and introgression within elite lines and recurrent selection population of key alleles contributing to tolerance to water deficit in rainfed rice / Agropolis Foundation, Embrapa, Capes / 2015-2017 / 170 k€

SEPYA, Breeding for resistance to blast and nitrogen use efficiency / Fonds de Soutien à l'Obtention Végétale / 2016-2019 / 400 k€

Transversal activities

Key resource person for the Cirad internal enquiry on the need on control facilities and for the development of a technical report describing the technical requirements of a new Cirad facility complex (controlled greenhouse compartments, reach-in and walk-in growth chambers, lab spaces) open to external users

Public Conferences and Open Forum, resource person

Organizer and Panelist, Roundtable Discussion 'Adaptation des Plantes au Changement Climatique', 22 February 2015, Salon International de l'Agriculture, CIRAD, Paris, France

Panelist, Workshop 'Agriculture et dérèglement climatique: quelles solutions pour l'avenir?', Regional Day for Interactions and Brainstorming, 19 June 2015, CERCOOP, Besançon, France

Panelist, Roundtable Discussion 'Changement climatique' during the Week of International Solidarity, 16 November 2015, COOPDEC, Rennes, France

Liste des publications

Peer-reviewed Journal papers

Bueno C, **Lafarge T**. Relevant traits for high yield in rice in the tropics as dependent on maturity groups and growing seasons. *Euphytica, under review*.

Lafarge T, Bueno CS, Frouin J, Jacquin L, Courtois B, Ahmadi N. 2017. Genome-wide association analysis for heat tolerance at flowering in rice detected a large set of genes involved in adaptation to thermal and other stresses. *Plos One, accepted with minor revision.*

Confalonieri R, Bregaglio S, Adam M, Ruget F, Li T, Hasegawa T, Yin X, Zhu Y, Boote K, Buis S, Fumoto T, Gaydon D, **Lafarge T**, Marcaida M, Nakagawa H, Ruane A, Singh B, Singh U, Tang L, Tao F, Fugice J, Yoshida H, Zhang Z, Wilson L, Baker J, Yang Y, Masutomi Y, Wallach D, Acutis M, Bouman B. 2016. A taxonomy-based approach to shed light on the babel of mathematical models for rice simulation. *Environmental Modelling & Software* **85**, 332-341.

Adriani DE, **Lafarge T**, Dardou A, Fabro, Clément-Vidal A, Yahya S, Dingkuhn M, Luquet D. 2016. The *qTSN* positive effect on panicle and flag leaf size is associated with an early down-regulation of tillering. *Frontiers in Plant Science*, **6**, 1197. doi: 10.3389/fpls.2015.01197

Adriani DE, Dingkuhn M, Dardou A, Adam H, Luquet D, **Lafarge T**. 2016. Rice panicle plasticity in Near Isogenic Line carrying a QTL for larger panicle is genotype and environment dependent. *Rice*, **9**, 28. doi: 10.1186/s12284-016-0101-x

Fabre D, Adriani DE, Dingkuhn M, Ishimaru T, Punzalan B, **Lafarge T**, Clement-Vidal A, Luquet D. 2016. qTSN4 effect on flag leaf size, photosynthesis and panicle size, benefits to plant grain production depending on its access to light. *Frontiers in Plant Science*, **7**, 623. doi: 10.3389/fpls.2016.00623.

Peraudeau S, **Lafarge T**, Roques S, Quinones CO, Clément-Vidal A, Ouwerkerk PBF, Van Rie J, Fabre D, Jagadish KSV, Dingkuhn M. 2015. Effect of Carbohydrates and Night Temperature on Night Respiration in Rice. *Journal of Experimental Botany*, **66**, 13, 3931-3944.

Peraudeau S, Roques S, Quinones CO, Fabre D, Van Rie J, Ouwerkerk BFP, Jagadish SVK, Dingkuhn M, **Lafarge T**. 2015. Increase in night temperature in rice enhances respiration rate without significant impact on biomass accumulation. *Field Crops Research*, **171**, 67-78.

Pasuquin EM, Hasegawa T, Eberbach P, Reinke R, Wade LJ, **Lafarge T**. 2013. Responses of eighteen rice (Oryza sativa L.) cultivars to temperature tested using two types of growth chambers. *Plant Production Science*, **16**, 217-225

Yoshimoto M, Fukuoka M, Hasegawa T, Matsui T, Tian X, Vijayalakshmi C, Singh MP, Myint TT, Weerakoon WMW, **Lafarge T**, Lur, HS, Tarpley L. 2012. MINCERnet: a global research alliance to support the fight against heat stress in rice. *Journal of Agricultural Meteorology*, **68**, 149-157.

Madan P, Jagadish SVK, Craufurd PQ, Fitzgerald M, **Lafarge T**, Wheeler TR. 2012. Effect of elevated CO_2 and high temperature on seed-set and grain quality of rice. *Journal of Experimental Botany*, **63**, 3843-3852.

Bueno C, Bucourt M, Kobayashi N, Inubushi K, **Lafarge T**. 2010. Crop productivity of contrasting rice genotypes grown under water-saving conditions and investigation of plant traits for adaptation. *Agricultural Water Management*, **98**, 241-250.

Bueno C, Pasuquin E, Tubaña B, **Lafarge T**. 2010. Improving sink regulation, and searching for promising traits associated with hybrids, as a key avenue to increase yield potential of the rice crop in the tropics. *Field Crops Research*, **118**, 199-207.

Fujita D, Ebron L, Araki E, Kato H, Kush G, Sheehy J, **Lafarge T**, Fukuta Y, Kobayashi N. 2010. Fine mapping of a gene for low-tiller number, *Ltn*, in japonica rice (*Oryza sativa* L.) variety Aikawa 1. *Theoretical and Applied Genetics*, **120**, 1233-1240.

Lafarge T, Seassau C, Martin M, Bueno C, Clément-Vidal A, Schreck E, Luquet D. 2010. Regulation and recovery of sink strength in rice plants grown under changes in light intensity. *Functional Plant Biology*, 37, 413-428.

Lafarge T, Bueno C. 2009. Higher performance of rice hybrids than of elite inbreds in the tropics: 2. Does sink regulation, rather than sink size, play a major role? *Field Crops Research*, **114**, 434-440

Bueno C, **Lafarge T**. 2009. Higher performance of rice hybrids than of elite inbreds in the tropics: 1. Hybrids accumulate more biomass during each phenological phase. *Field Crops Research*, **112**, 229-237

Ainsworth EA, Beier C, Calfapietra C, Ceulemans R, Durand-Tardif M, Farquhar GD, Godbold DL, Hendrey GR, Hickler T, Kaduk J, Karnosky DF, Kimball BA, Korner C, Koornneef M, **Lafarge T**, Leakey ADB, Lewin KF, Long SP, Manderscheid R, McNeil DL, Mies TA, Miglietta F, Morgan JA, Nagy J, Norby RJ, Norton RM, Percy KE, Rogers A, Soussana JF, Stitt M, Weigel HJ, White JW. 2008. Next generation of elevated [CO2] experiments with crops: a critical investment for feeding the future world. *Plant, Cell and Environment*, **31**, 1317-1324.

Pasuquin, E., **Lafarge T**, Tubana B. 2008. Transplanting young seedlings in irrigated rice fields: early and high tiller production enhanced grain yield. *Field Crops Research*, **105**, 141-155

Wiangsamut B, Mendoza TC, **Lafarge T**. 2006. Growth dynamics and yield of rice genotypes grown in transplanted and direct-seeded fields. *Journal of Agricultural Technology*, **2**, 299-316.

Lafarge T, Broad I, Hammer G. 2002. Tillering in grain sorghum over a wide range of population densities: identification of a common hierarchy for tiller emergence, leaf area development and fertility. *Annals of Botany*, **90**, 87-98.

Lafarge T, Hammer G. 2002. Tillering in grain sorghum over a wide range of population densities: modelling dynamics of tiller fertility. *Annals of Botany*, **90**, 99-110.

Lafarge T, Hammer G. 2002. Predicting plant leaf area production: shoot assimilate accumulation and partitioning, and leaf area ratio, are stable for a wide range of sorghum population densities. *Field Crops Research*, **77**, 137-151.

Lafarge T, Tardieu F. 2002. A model co-ordinating the elongation of all leaves of a sorghum cultivar was applied to both Mediterranean and Sahelian conditions. *Journal of Experimental Botany*, **53**, 369, 715-725.

Lafarge T, de Raïssac M, Tardieu F. 1998. Elongation rate of sorghum leaves has a common response to meristem temperature in diverse African and European environmental conditions. *Field Crops Research*, **58**, 69-79.

Tardieu F, **Lafarge T**, Simonneau Th. 1996. Stomatal control by fed or endogenous xylem ABA in sunflower: interpretation of correlations between leaf water potential and stomatal conductance in anisohydric species. *Plant, Cell and Environment*, **19**, 75-84.

Book Chapters

Valluru R, Reynolds MP, **Lafarge T.** 2015. Food security through translational biology between wheat and rice. In: Martin Parry, William Davies (Eds), *Food and Energy Security*. 2015. John Wiley & Sons, Ltd. and the Association of Applied Biologists. Published 2015 by Blackwell Publishing Ltd.

Lafarge T, Julia C, Baldé A, Ahmadi N, Muller B, Dingkuhn M. 2015. Stratégies d'adaptation du riz en réponse à la chaleur au stade floraison. In: Emmanuel Torquebiau (Ed.), *Changement climatique et agricultures du monde*. Agricultures et défis du monde, Collection Cirad-AFD, Editions Quae, Versailles, 2015. Chapter 3, pp. 37-49.

Dreccer MF, Bonnett D, **Lafarge T**. 2012. Plant breeding under a changing climate. In: Robert A. Meyers (Ed.), *Encyclopedia of Sustainability, Science and Technology*, **11:** 8013-8024. Springer Science - Verlag

Lafarge T, Peng S, Hasegawa T, Quick WP, Jagadish SVK, Wassmann R. 2011. Genetic adjustment to changing climates: rice. In: Shyam Yadav, Robert Redden, Jerry Hatfield, Hermann Lotze-Campen and Anthony Hall (Eds), *Crop Adaptation to Climate Change*. 2011 John Wiley & Sons, Ltd. Published 2011 by Blackwell Publishing Ltd. Chapter 12, pp 298-313.

Redden RJ, Yadav SS, Hatfield JL, Prasanna BM, Vasal SK, **Lafarge T**. 2011. The potential of climate change adjustment in crops: a synthesis. In: Shyam Yadav, Robert Redden, Jerry Hatfield, Hermann Lotze-Campen and Anthony Hall (Eds), *Crop Adaptation to Climate Change*. 2011 John Wiley & Sons, Ltd. Published 2011 by Blackwell Publishing Ltd. Chapter 24, pp 482-494.

Lafarge T, Siband PL, Bueno CS, Samson M. 2006. Plant traits accounting for superior yield in hybrid rice. In: Despréaux Denis (ed.), Frison Emile A. (ed.), Hubert Bernard (ed.), Lantin Manuel M. (ed.). *La France et le CGIAR: Delivering scientific results for agricultural development*. Washington: CGIAR, p. 41.

Oral presentations in conferences and international workshops

Lafarge T. 2016. The difficulties and constraints of phenotyping for high quality phenomic data. Paper presented at the International Gene-based Modeling Workshop, 1-3 November 2016, Gainesville, USA

Lafarge T, Julia C, Peraudeau S, Ahmadi N, Dingkuhn M. 2016. Rice adaptation to day and night heat - Consequences for modeling. Invited paper at the 36th Rice Technical Working Group Meeting, 1-4 March, Galveston, USA

Lafarge T, Julia C, Ahmadi N, Dingkuhn M. 2015. Rice adaptation pathways in response to heat stress at anthesis. Invited paper presented at the Third International Plant Physiology Congress, 11-14 December 2015, New Delhi, India

Lafarge T, Bueno C. 2014. Relevant plant traits for high yielding rice in the tropics are different depending on the maturity group and the cropping season. Selected paper presented at the Session "*New Varieties and Rice Breeding*". The 4th International Rice Congress, 27 October - 1 November 2014, BITEC, Bangkok, Thailand, IRC14-0850.

Dingkuhn M, Luquet D, Laza R, Kumar U, Adriani DE, Peraudeau S, **Lafarge T**. 2014. Rice yield potential : can integration of 'omics' and ideotype modeling break new ground ? Invited paper presented at the Symposium "*Increasing yield potential: from physiological processes to ideotyping*". The 4th International Rice Congress, 27 October - 1 November 2014, BITEC, Bangkok, Thailand. IRC14-1192.

Tardieu F., **Lafarge T.** 2012. Concepts, approches et outils pour la conception et le développement d'idéotypes variétaux adaptés à une agriculture durable: (Résumé). In: INRA ; CIRAD. Les Rencontres INRA: Améliorer les céréales pour une agriculture durable dans un contexte changeant, Paris, France, 2 mars, 2012. Les rencontres INRA, 2012-03-02, Paris, France.

Lafarge T, Bueno CS. 2012. Exploiting phenotyping diversity of hybrid rice: identification of novel traits of interest for high yield. Sixth International Hybrid Rice Symposium, 10-12 September 2012, Hyderabad, India

Tittonell P, Affholder F, Scopel E, **Lafarge T**, Corbeels M 2011. Yield gap assessments in tropical smallholder agriculture. Yield Gap Assessment Workshop, Beijing, 31rst August 2011.

Lafarge T. 2011. Breeding for a 2030 world: some issues and opportunities. Global Science Conference on Climate-Smart Agriculture, 24-26 October 2011, Ede-Wageningen, The Netherlands

Dingkuhn M, Soulié JC, **Lafarge T**. 2011. Samara V2: A cereal crop model to study G x E x M interaction and phenotypic plasticity, and explore ideotypes. AgMIP Rice International Workshop, 28-30 August, Beijing, China

Luquet D, Soulié JC, Rebolledo MC, Pradal C, **Lafarge T**, Dingkuhn M. 2011. Modelling rice morphogenesis and its G x E regulation with Ecomeristem. AgMIP Rice International Workshop, 28-30 August, Beijing, China

Bueno CS, Wiangsamut B, **Lafarge T.** 2010. Expanding alternate wetting and drying and expanding its productivity in irrigated rice: identification of required plant traits and suitable soil types. Third International Rice Research Congress, 8-12 November 2010, Hanoi, Vietnam.

Lafarge T, Luquet D, Dingkuhn M, Soulié JC, Rouan L, Julia C, Rebolledo MC, Oriol P, Muller B. 2010. Predicting crop productivity and adapting the rice plant to changing climates: the importance of modeling. Third International Rice Research Congress, 8-12 November 2010, Hanoi, Vietnam.

Dingkuhn M, **Lafarge T.** 2010. L'adaptation du sorgho et du riz au changement climatique: Stratégies et opportunités contrastées. In : *Atelier Cirad-Iddri "Agriculture, développement et changement climatique", 07 juillet 2010, Montpellier, France*. s.l. : s.n., 1 diaporama (22 vues). Atelier Cirad-Iddri Agriculture, développement et changement climatique, 2010-07-07, Montpellier, France.

Lafarge T. 2009. Beyond tillering: yield slipping down the sink. IRRI Thursday Seminar Series, International Rice Research Institute, 3 December 2009, Los Baños, Philippines.

Lafarge T, Fitzgerald M, Heuer S, Howell GJ, Krishna JSV, Li T, Peng S, Redoña E, Sumfleth K, Wassmann R. 2009. Adapting the rice crop to hotter environments: Current and future activites at IRRI. In: T. Hasegawa and H Sakai (Eds), Crop Production under Heat Stress: Monitoring, Impact Assessment and Adaptation, pp. 65. Proceedings of the International MARCO Symposium, 5-9 October 2009, Tsukuba, Japan. National Institute for Agro-Environmental Sciences (NIAES), Tsukuba, Japan, 90 pp.

Meinke H, Bastiaans L, Bouman B, Dingkuhn M, Gaydon D, Hasegawa T, Heinemann AB, Kiepe P, **Lafarge T**, Luquet D, Masood A, van Oort P, Rodenburg J, Yan J, Yin X. 2009. An international collaborative research network helps to design climate robust rice systems. In: T. Hasegawa and H Sakai (Eds), Crop Production under Heat Stress: Monitoring, Impact Assessment and Adaptation, pp. 1-11. Proceedings of the International MARCO Symposium, 5-9 October 2009, Tsukuba, Japan. National Institute for Agro-Environmental Sciences (NIAES), Tsukuba, Japan, 90 pp.

Yoshimoto M, Fukuoka M, Hasegawa T, Tian X, Singh MP, Daw TTM, Weerakoon WMW, **Lafarge T**, Lur HS, Tarpley L, Matsui T, Kobayasi K, Kuwagata T. 2009. Multi-site monitoring of heat stresses and micrometeorological conditions in the rice plants communities under various climates - The micrometeorological measurements systems for a common measure oft he paddy environments. In: T. Hasegawa and H Sakai (Eds), Crop Production under Heat Stress: Monitoring, Impact Assessment and Adaptation, pp. 53-56. Proceedings of the International MARCO Symposium, 5-9 October 2009, Tsukuba, Japan. National Institute for Agro-Environmental Sciences (NIAES), Tsukuba, Japan, 90 pp.

Luquet D, Soulié JC, **Lafarge T**, Dingkuhn M. 2009. Modelling rice phenotyping plasticity in diverse climates using EcoMeristem: model evolution and applications to rice improvement. In: T. Hasegawa and H Sakai (Eds), Crop Production under Heat Stress: Monitoring, Impact Assessment and Adaptation, pp. 74. Proceedings of the International MARCO Symposium, 5-9 October 2009, Tsukuba, Japan. National Institute for Agro-Environmental Sciences (NIAES), Tsukuba, Japan, 90 pp.

Lafarge T, Bueno C, Pasuquin E, Wiangsamut B. 2009. Biomass accumulation and sink regulation in hybrid rice: consequences for breeding programs and crop management. In: F Xie and B Hardy (Eds), Accelerating Hybrid Rice Development, pp. 453-474. Proceedings of the International Symposium on Hybrid Rice, 11-15 September 2008, Changsha, Hunan, China. International Rice Research Institute, Los Baños, Philippines, 698 pp.

Lafarge T, Peng S, Virk P, Kang KH, Kobayashi N. 2009. Strategies for increasing yield potential. IRRI Annual Program Review, International Rice Research Institute, 13-17 April 2009, Los Baños, Philippines.

Peng S, Xie F, **Lafarge T**, Virk P, Dobermann. 2008. Integration of breeding and physiology for developing new rice varieties with higher yield potential. NSFC-IRRI Joint Workshop on Rice Science, 17-19 December 2008, China National Rice Research Institute, Hangzhou, China.

Lafarge T, Bueno C, Bucourt M, Wiangsamut B. 2007. Quantifying the morphological plasticity of plant response to alternate wetting and drying with regard to genotype characteristics and soil texture. IRRI-Japan Annual Workshop, 11 December 2007, International Rice Research Institute, Los Baños, Philippines.

Lafarge T, Bueno C, Pasuquin E. 2007. Increasing yield potential: lessons learnt from inbreds and hybrids. IRRI Annual Program Review, International Rice Research Institute, 20-23 November 2007, Los Baños, Philippines.

Lafarge T, Pasuquin E, Wiangsamut B. 2007. Differential effects of day and night temperature on leaf elongation and determination of apparent base temperature for contrasted genotypes. Cool Rice for a Warmer World, Wuhan, China, 26-29 March 2007.

Lafarge T, Pasuquin E, Susanti Z, Tubana B, Bueno C. 2006. Achieving higher grain yield through integrated crop establishment in irrigated rice fields. Second International Rice Research Congress, 9-13 October 2006, New Delhi, India

Lafarge T, Susanti Z, Pasuquin E. 2006. Can higher grain yield be achieved in irrigated rice fields through desirable nursery management? The 39th Annual Scientific Conference of the Crop Science Society of the Philippines, 8-12 May 2006, Puerto Princesa, Philippines.

Lafarge T, Pasuquin E, Bueno C, Susanti Z, Tubana B, Bertheloot J, Seassau C, Shah T, Wiangsamut B. 2005. Enhancing crop performance: the challenge of integrating crop establishment strategies with effective plant traits. IRRI Thursday Seminar Series, International Rice Research Institute, 17 November 2005, Los Baños, Philippines.

Rapport sur les stages effectués au cours des études

1990. Contribution à l'étude des mécanismes physiologiques d'adaptation à la sécheresse chez le blé dur (*Triticum durum* Desf.). **Laboratoire des Céréales, Centre INRA-ENSA de Montpellier**, encadrement Philippe Monneveux (1 mois).

Le programme sélection du blé dur a besoin d'utiliser des caractères simples, indicateurs de l'adaptation à la sécheresse, pour déterminer la diversité de réponse au sein de la population de travail et identifier des lignées prometteuses. Les indicateurs physiologiques suivis ont été le potentiel hydrique foliaire, la fluorescence, la concentration en proline foliaire, et la température des feuilles, et les indicateurs morphologiques ont été la présence de barbes et la manifestation ou non de verse. L'objet de ce stage m'a principalement permis de me familiariser avec diverses outils de mesure comme la presse à membrane, le fluorimètre, la lecture de densité optique par spectrophotométrie, le thermomètre infrarouge, et une grille de notation de la manifestation de la verse établit sur une échelle de 0 à 5.

1993. Effect of abscisic acid pre-treatment on the effect of salinity on various cultivars of rice (*Oryza sativa* L.). **School of Biological Sciences, University of Sussex, UK**, encadrement Tim Flowers (1 mois)

Dans les sols à haute teneur saline, la plante de riz régule sa concentration en sel dans les feuilles par un ajustement osmotique dans les zones de croissance. La photosynthèse, ainsi que la croissance, diminuent. Si les teneurs en sel du substrat sont trop élevées, comme par exemple 50 mM au stade germination, le taux de mortalité des plantes est notoire. Dans le but d'augmenter la résistance du riz au sel, l'objectif de ce stage était de quantifier l'influence d'une imbibition des semences de la variété IR36 à l'acide abscissique (ABA) en amont du semis. Les graines ont été imbibées pendant 24 heures dans une solution d'ABA à 10^{-3}M, traitement qui n'affecte pas le taux de germination, mais augmente la biomasse racinaire et aérienne stimulées par la concentration élevée d'ABA. Malgré la présence de NaCl dans la solution nutritive, l'imbibition préalable à l'ABA rétablit le poids des parties aériennes et entraîne une baisse de la concentration interne en ions Na^+ chez la plante traitée comparée à la plante témoin.

1994. Contrôle de la conductance stomatique du tournesol (*Helianthus annuus* L.) soumis à une contrainte hydrique: effets respectifs du déficit de saturation de l'air et de la concentration xylèmique en ABA. **Laboratoire du LEPSE** (Etude des Plantes sous Stress Environnementaux), **Centre INRA-ENSA de Montpellier**, encadrement François Tardieu (6 mois)

L'objectif de ce stage était de déterminer si un message racinaire aurait une influence sur l'ouverture stomatique de plantes anisohydriques (comme le tournesol) se développant en conditions de sécheresse. Des conditions de culture contrastées de déficit de pression de vapeur saturante de l'air, d'états hydriques du sol et teneurs en acide abscissique (ABA) des plantes (par alimentation d'ABA exogène de plantes sous perfusion) ont été mises en place. La conductance stomatique, le potentiel hydrique foliaire et la concentration en ABA du xylème ont été mesurés et analysés. La concentration stomatique a été fortement corrélée à la concentration en ABA dans le xylème, mais sa corrélation avec le potentiel hydrique foliaire a été différente pour chacune des situations explorées. Le potentiel hydrique foliaire du tournesol n'intervient donc pas dans la relation entre conductance stomatique et concentration en ABA dans le xylème : la conductance stomatique est contrôlée par un message chimique racinaire indépendamment du potentiel hydrique foliaire : le tournesol est une plante anisohydrique.

Activités d'encadrement

Co-encadrement de thèses de Doctorat

Adriani, Dewi Erika. Analysis of the developmental plasticity of the rice panicle, and its control by plant sugar status, in materials introgressed with the qTSN4 QTL. PhD Thesis. Cotutelle Program between Montpellier SupAgro, Montpellier, France, and Bogor Agricultural University, Bogor, Indonesia, 2012-2015, 124 pp.

Publications effectuées:

Adriani DE, **Lafarge T**, Dardou A, Fabro, Clément-Vidal A, Yahya S, Dingkuhn M, Luquet D. 2016. The *qTSN* positive effect on panicle and flag leaf size is associated with an early down-regulation of tillering. *Frontiers in Plant Science*, **6**, 1197. doi: 10.3389/fpls.2015.01197

Adriani DE, Dingkuhn M, Dardou A, Adam H, Luquet D, **Lafarge T**. 2016. Rice panicle plasticity in Near Isogenic Line carrying a QTL for larger panicle is genotype and environment dependent. *Rice*, **9**, 28. doi: 10.1186/s12284-016-0101-x

Fabre D, Adriani DE, Dingkuhn M, Ishimaru T, Punzalan B, **Lafarge T**, Clement-Vidal A, Luquet D. 2016. qTSN4 effect on flag leaf size, photosynthesis and panicle size, benefits to plant grain production depending on its access to light. *Frontiers in Plant Science*, **7**, 623. doi: 10.3389/fpls.2016.00623.

Peraudeau Sébastien. Réponse de la respiration à l'augmentation de la température nocturne chez le riz: production de biomasse et de grains et conséquences pour les modèles de culture. PhD Thesis. Université Montpellier 2, Montpellier, France, 2011-2014, 132 pp.

Publications effectuées:

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Encadrement de thèses de Master

Bucourt Marie. 2006. Increasing water productivity in irrigated rice (*Oryza sativa* L.) fields: Characterization of morphological response of five contrasted genotypes to alternate wetting and drying. Master Thesis, University of Sciences and Techniques of Languedoc (USTL) and National Engineering School of Agronomy (ENSAM), Montpellier. Internship performed at IRRI, Philippines, from January to June 2006, 23 pp.

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Participation à des jurys de thèses de Doctorat

Adriani, Dewi Erika. Analysis of the developmental plasticity of the rice panicle, and its control by plant sugar status, in materials introgressed with the qTSN4 QTL. PhD Thesis. Cotutelle Program between Montpellier SupAgro, Montpellier, France, and Bogor Agricultural University, Bogor, Indonesia - 25 November 2015, Bogor Agricultural University, Indonesia

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An overview of my cursus

I started my cursus working on sorghum during my PhD (1994-1998) when I studied the dynamics of leaf area production of one West African cultivar. This was analyzed at plant level, looking at rates of leaf emergence and leaf elongation at different position on the stem, and with careful analysis of developmental and elongation processes response to local temperature. A large range in temperature was created through scattered sowing dates over the year in Mali and some additional in Montpellier. I moved then to Australia for a year (1998-1999) where I did one postdoctoral study on sorghum as well, still looking at leaf area production, but focusing on the tillering dynamics under a range of plant densities and of tiller removal treatments. At the end of my postdoc, I came back to Montpellier where I got an ATER position at University Montpellier 2 in Plant Physiology for two years. Soon after the end of my contract, I got hired by Cirad (2002) to work on rice and move to IRRI in the Philippines to contribute to the increase in rice yield under favorable conditions. After some time to get familiar with rice culture, with Asia and with the CG system, I decided to keep tillering as one of the main focus of my studies and initiated first some work on the nursery management, evaluating several ways of running the nursery and analyzing their effects on crop performance. Also, quickly after my arrival at IRRI, I decided to exploit the difference in performance between hybrid rice and improved varieties to reveal traits/processes subtending higher yield. At the same time, I have also looked at the effect of contrasted plant density and shading on crop development, focusing on tillering. During this period, I was the main adviser of one PhD study conducted by one of my IRRI staff registered in a University in Japan. I became also involved in searching for genotypes adapted to the Alternate Wetting and Drying water management, a system that significantly reduces water use by 10 to 20% while maintaining grain yield. At the end of my stay, I got more interested with issues related to adaptation to Climate Change, where temperature was a key constraint. I left IRRI in 2010 and get back to Cirad to become the leader of the PAM team of the newly formed UMR AGAP during four years. During that time, I co-supervised two PhD studies conducted in Montpellier. Late 2014, I expressed my wish of going back overseas to get closer to the field and decided to leave the leadership of the team. In the following part of my manuscript, I mainly organized the presentation of my research activities focusing on rice, but sorghum results were confronted to those of rice whenever it was available and interesting. In the description of the results, I have included some non-published data for which the relevant figures were inserted.

Analysis of the scientific activities

Sink size of a rice crop, defined as the total number of spikelets at flowering, is considered as the primary determinant of grain yield under favorable environments (Fischer 1983; Kropff et al. 1994): high yielding ability is well correlated with large sink size in temperate (Nagata 2006), subtropical (Wu et al. 2008; Xiong et al. 2013), and tropical (Ying et al. 1998; Yang et al. 2007) environments. This has been confirmed when sink size limitation due to higher temperature accelerated plant maturity despite maintenance of leaf photosynthesis activity (Kim et al. 2011). Accordingly, breeding programs for higher yield potential in rice have been mainly driven by increasing sink size (Yang et al. 2002). However, this strategy often reduced the breeding target to increasing one individual yield component without addressing any compensation phenomenon (Kovi et al. 2011; Fujita et al. 2013) or any relevance of subtending yield formation processes (Ying et al. 1998; Laza et al. 2004; Yang et al. 2007; Ohsumi et al. 2011). On one hand, compensation between yield components is widely expressed across genotypes through contrasted combinations of components (Huang et al. 2011; Dingkhun et al. 2015). As an example, the breeding program for NPTs (Dingkuhn et al. 1991) and super hybrid rice (Yang et al. 2002) targeted bigger but fewer panicles; however, this was associated with lower filling capacity (Peng et al. 1999 and Laza et al. 2003, for NPTs; Ao et al. 2008, for super hybrid rice). Similarly, introgression of a genetic segment driving the increase in one component, such as the number of spikelets per panicle (Fujita et al. 2009, 2012), translated rarely into higher performance at the crop level, which was prone to G x E interaction (Ohsumi et al. 2011; Okami et al. 2015). On the other hand, as grain yield is well correlated with sink size (Liang et al. 2001; Kim et al. 2011), and sink size is already fixed at flowering, pre-flowering traits appear instrumental in determining grain yield in favorable conditions. In fact, sink could be dimensioned in line with the supply capacity of the plant during the pre-flowering phase.

Higher crop growth rate (CGR) during the 14 days prior to heading has already been identified as a key early plant trait favoring panicle growth and sink size under temperate (Takai et al. 2006; Kamiji et al. 2011) and subtropical (Nagata 2006; Xiong et al. 2013) environments, and across environments (Ying et al. 1998). This was derived from higher radiation-use efficiency (Takai et al. 2006), inducing higher leaf area index (LAI) (Wu et al. 2008) with larger accumulation of non-structural carbohydrates (NSC) in the leaves, and translocation to the panicle (Takai et al. 2006; Xiong et al. 2013). Also under subtropical environments, longer crop (Zhang et al. 2009; Huang et al. 2013) and green leaf area (Ying et al. 1998; Wu et al. 2008) duration promoted biomass accumulation and yield. In the tropics, however, even if the possible occurrence of higher CGR (Sheehy et al. 2001; Yoshida et al. 2006) supported biomass growth as a target for higher yield (Peng et al. 1999), biomass allocation rather than biomass production was stated as a crucial trait for higher yield. This was the case in the dry season, but also in the wet season despite a lower contrast in crop yield (Laza et al. 2003; Yang et al. 2007).

These observations raise the question whether resource acquisition or sink size, biomass accumulation or biomass partitioning, is the main driver of grain yield. Sink size, indeed, appears to be adjusted (i) to the actual growing conditions of the crop, since low density crops develop a much higher spikelets number per plant than highly dense crops (Sheehy et al., 2001), (ii) to the intrinsic ability of the plant to accumulate biomass, with sink size increasing as flag leaf size increased (Yue et al., 2006), and (iii)

to the intrinsic ability of the plant to partition biomass, with sink size increasing as carbohydrate storage capacity before heading increased (Ishimaru et al., 2005). Considering the strong trade-off between yield components that prevents from selecting one of them as a target, and how early traits can be involved in the establishment of grain yield and contribute to higher performance, it is legitimate to analyze the ability of the plant in managing its sink efficiently by taking into account early component traits, which may directly contribute to the crop performance, and be a relevant tool to compare genotypes behavior. Among early component traits, tillering is probably the most plastic trait in response to the source:sink interactions. The hypothesis here is that tillering dynamics can be considered as a key process to better understand source:sink interactions within then plant. In particular, this study will address the main following issues: (i) Is tillering a relevant trait to compare genotypes in their ability to govern their sink efficiently and to produce higher yield? (ii) Which tillering pattern is correlated with higher yield? One of the entry point of this work is the comparison of process-based performances between hybrid rice and improved inbreds: the stable consistency of higher yields observed with hybrids make it a strong basis to compare the course of sink emergence and sink activity, and the priority in-between sinks, and their effect on yield elaboration processes. These main traits related to tillering will also be compared between rice and sorghum canopies, high-tillering and low-tillering crops, so that tillering-related processes will be observed in a wide range of situations, and any common pattern detected with rice and sorghum will be considered as quite powerful.

I - Sink regulation as a key process for high yield

The establishment of many successive sinks of the plant occur during the vegetative and reproductive phases. In the above-ground canopy, it includes the production of leaves on one culm, the production of tillers, the vigor of the organs, the storage of resources, the elongation of internodes, the elaboration of the panicle. Because of the many sinks, with distinct strength and duration of activity, that can be active simultaneously or at different time, the regulation between all of these sinks may be highly different relative to the genotypes and appear as essential in the establishment of grain yield. These two early phases are appropriate to analyze and understand how sink regulation is governed with respect to sink timing and priority, how plasticity of some of sinks like tillering is affected by growth conditions, and to identify which traits/processes are favorable to final yield.

Prior to study the competition between sinks, it is useful to position in time the phenological events and the growth period of the different organs (i.e. the sinks). It also helps to visualize which sinks are growing at the same time (then are in competition for the access to resources), what their period of growth is (this can help evaluating their demand for resources), and how growth pattern of the different tillers may differ from each other. This can also help evaluating which tillers are non-priority in case of resources storage. This also requires accounting for the temperature effect on crop phenology in the calculation of thermal time in order to compare different growing conditions and G x E analyses.

A - Environment characterization and the importance of microclimate

The plant is sensitive to the conditions that are in its direct proximity and that are even modified by the crop itself: the crop (i) reduces, by its physical stature, the influence of the air movements within its own canopy and (ii) modifies these conditions through transpiration which increases local air humidity and decreases local temperature by consuming energy. Below is the description of two examples I worked on, one at early stage, one at a later stage, that highlights how relevant consideration of the microclimate (here the local temperature) allows to understand the direct effect of growing conditions on plant behavior which provides some bases for further applications in phenotyping and crop modeling.

Early stage

The apical meristem is the key organ at early stage, being the site controlling plant phenology and organ production, i.e. leaf and axillary bud initiation, the formation of the leaf elongation zone and the tiller emergence rate from the axillary buds. Eventually, meristem temperature drives the rate of leaf initiation, tiller initiation, and leaf elongation. Until internodes start to elongate, the meristem is located at the base of the plant and so most of these processes depend on soil temperature. In a set of experiments I have conducted on sorghum in the field in Mali (Sotuba research station) and Montpellier (Lavalette research station), and in the growth chamber, the response of leaf appearance and elongation rate to meristem temperature was consistent in the different locations and seasons (Lafarge et al, 1998). This consistency was also extended to the elongation of leaves located at different positions on the stem when evaporative demand (VPD) was lower than 2.5 kPa. Under high evaporative demand, although elongation rate was lower than that expected at the same temperature under low VPD, the difference could actually be directly related to the actual VPD (Lafarge et al, 1998). This conclusion confirms the importance of analyzing plant growth and development until internode elongation with respect to meristem temperature, assimilated to soil temperature in the case of sorghum and rainfed rice, to water temperature in the case of irrigated rice. Conducting such analyses with respect to air temperature above the canopy would lead to improper consideration of the temperature effect and would prevent from any plant diversity and G x E analysis.

A common value was used as base temperature for these distinct processes as the relationships remained linear in sorghum, over the whole studied temperature range from 13 to 32°C for leaf elongation, and over the range from 13 to 27°C for leaf appearance when this was measured before stem elongation, and since the x-intercepts did not differ in a covariance analysis (Lafarge et al, 1998). It was 10.8 °C in the case of sorghum in the former study. Because I have not conducted such detailed analysis anymore, I used widely the value of 11 °C for sorghum in Australia and for irrigated rice. The calculation of thermal time without corrections for high VPD conditions at high temperature was finally an appropriate way to account for the timing of plant development and growth in the other conditions I have experienced where VPD conditions did not exceed 2 kPa, and was then used thereafter.

Late stage

Spikelet fertility, potentially affected at the time of microsporogenesis (booting stage) and anthesis (flowering time), is recognized as being strongly affected by high temperature. Similarly to the response of vegetative growth to meristem temperature, spikelet fertility has to be analyzed with respect to the canopy temperature. Indeed, due to evapotranspiration, canopy temperature can be lower than that of air temperature measured 2 m above the canopy, with the range of difference between air and canopy temperatures depending on air humidity (Yoshimoto et al, 2012). These conclusions were reported from a network monitoring the rice canopy thermal environment in paddy

fields and assessing the magnitude of temperature differences between climatic zones. The importance of taking air relative humidity into account in assessing the capacity of the plant to cool its panicles through transpiration was confirmed in a devoted study focused on the prediction of spikelet fertility in rice. The range in variation between soil (water), mid-canopy, canopy and air temperature was studied in details across sites differing strongly in air humidity: Los Baños, Philippines (humid environment), Camargue, France (intermediate) and the Senegal River valley (dry environment) with VPD values ranging from 1 kPa in the Philippines up to 4 kPa in Senegal (Lafarge et al, 2015). In Senegal because of the high evaporative demand, the canopy temperature fluctuated in-between that of the water and of the air so that it was always lower than that of the air, while in the Philippines it was systematically close to that of the air because of the low evaporative demand (Lafarge et al, 2015, extracted from Julia and Dingkuhn, 2013). In fact, closely interrelated variables like air VPD (65%) and air relative humidity (64%) were by far the most important explanatory variables of the panicle to air temperature difference, leading to a range of variation of panicle temperature relative to that of the air from 9 °C lower to 2 °C higher. A significant positive correlation was obtained between spikelet sterility rate and maximum panicle temperature at flowering across environments and varieties, whereas no correlation was obtained when the maximum reference temperature was that of the air (Lafarge et al, 2015, extracted from Julia and Dingkuhn, 2013). On this basis, prediction of 50 % sterility occurs at a panicle temperature of 33–34 °C, which is clearly lower than the ranges published in the literature.

Canopy temperature is, by extension, the key driver of internode elongation and of leaf elongation while internode are elongating. This is often the stage when the apical meristem is developing into an inflorescence and is pushed by the subtending elongating internodes from the soil surface to the top layer of the canopy.

Discussion

Taking into account microclimate conditions is essential to analyze the direct effect of growing conditions on relevant plant traits and identify stable relationships over contrasted conditions. Revealing such relationships, and their key parameters, is a requirement for the analysis of Genotype x Environment interactions, the dissection of the genetic diversity and the integration of genetic diversity within crop models. Each genotype is then characterized by a set of parameters values.

B - Coordination of the growth duration of each organ of the plant

The phytomer of grasses is composed of a blade, a sheath, a node, potentially an internode, and an axillary bud, however, the structures demanding for carbohydrate resources are only the blade, the sheath and the internode in case this one elongates. The elongation of these structures are known to be well coordinated in time within a plant. This coordination can be used as a basis to characterize the duration of elongation of each organ and which organs of the plant are elongating at a given time. The strong morphological differences between sorghum and rice, rice being short and high tillering while sorghum developing several long internodes but very few tillers, makes their comparison suitable to detect any similarities in their coordination: this would highlight the common bases of cereal development and reinforce the interest of using this type of framework as a pillar for crop models and diagnosis analyses.

Case of sorghum

Elongation of the blades, sheaths and internodes in sorghum is characterized by an exponential phase (establishment of the cell number of the elongating zone) and a linear phase (elongation of a stable number of cells in time) until the cessation of elongation (Lafarge and Tardieu, 2002). At the phytomer level, it is noteworthy that elongation of each of these three organs occurs in a sequential manner, with the linear elongation phase of the sheath starting at the end of that of the blade, and the linear elongation phase of the internode starting at the end of that of the sheath (Figure 1). The same remark applies to the cascade of exponential elongation in time (Lafarge and Tardieu, 2002). Sorghum is particularly well designed for studying the coordination of phenological events as one culm can produce a large number of phytomers (24 under Montpellier conditions for the variety I have worked with), stem length can reach high values (about 2 m in Montpellier, but 3 to 4 m in Mali for the same variety) and several internodes elongate. In particular, the coordination of events would explain why the blade of the last leaves, and namely of the flag leaf (the last lead produced by the culm), is shorter than that of the previous phytomer, while their sheath is rather longer than that of the previous phytomer. The cessation of elongation of the blades of the last phytomers is even simultaneous and is most probably associated with the quick increase in stem length (with more sheaths elongating at the same time) before the panicle emerges from the whorl. In fact while blade length is decreasing and sheath length increasing with the upper phytomer position, the cumulated length of the blade and sheath of each of the last phytomers is about similar with phytomer position (Figure 2). It is a strong hypothesis that the reduction in total length of phytomers at position higher than 14 is the result of the competition between phytomers elongation and panicle elongation. Overall, a model coordinating the elongation events at culm level highlights that end of blade elongation and the transition between the exponential and linear elongating phases of the sheath are concomitant, the end of sheath elongation and the transition between the exponential and linear elongating phases of the internode are concomitant (Figure 3). Interestingly, ligule appearance is about simultaneous with the end of internode elongation. The slopes of the end of elongation of the blades, sheaths and internodes were similar starting at about phytomer at position 12 before the end of elongation of the upper blades stops almost simultaneously.

Case of rice

Similarly to sorghum, elongation of each of these three organs of one phytomer occurs in a sequential manner, with the linear elongation phase of the sheath starting at the end of that of the blade, and the linear elongation phase of the internode starting at the end of that of the sheath (Figure 4). This was observed on the main tiller of the most rice popular variety in Asia, IR64, from one of the upper phytomers of the culm as only three to four internodes elongate in rice. The model coordinating the elongation events at culm level highlights also the succession of growth periods of the succeeding organs at each phytomer (Figure 5) for those leaves that were bearing elongated internodes, so phytomers position 12 to 17. Although data respective of each organ are representing the total period of organ elongation (the addition of the duration of the exponential and linear phases), it appears also in rice that the time between the end of blade and sheath elongation is about stable whatever the phytomer, except in the case of the flag leaf, phytomer 17 in this example, where sheath elongation is appreciably longer than that of the previous leaves. The elongation of the panicle, here represented at phytomer position 18, was concomitant with the elongation period of the blade and sheath of the flag leaf, and was over whereas the internodes of the three upper phytomers were still elongating (Figure 5). The end of elongation of the peduncle was earlier than that of the internodes of the upper two phytomers. It highlights also that panicle initiation (which corresponds here to the start of panicle

elongation) occurs at the end of elongation of the blade of the third phytomer from top, and at the end of the elongation of the sheath of the fourth phytomer from top.

Discussion

The elongation phases of the organs of the many phytomers of a culm are highly coordinated, as observed on sorghum and rice. The sequential pattern of the phases of elongation was observed with both species. This model, by positioning the duration of the elongation phases with crop cycle, explains largely the distribution patterns of the final length of the organs of a culm observed a posteriori, taking into account that organ elongation rate does not differ much in-between phytomers except that of the very early phytomers. Some visual non-invasive observations, like the leaf ligule emergence, can be used as a reference to position the elongation phases in time.

This model is of great use for crop models developed at the phytomer level in that it positions in time the many elongation phases of each organ of the main tiller, in case no transient constraint occurs. It provides the timing of the start and of the end of the succeeding vegetative sinks of the culm and, by this way, can drive the distribution of biomass partitioning in-between sinks and indicate the organ that shall be sacrificed in case of a shortage of resources. By comparing the pattern of final organ length at maturity, this model can also be used *a posteriori* to identify the time at which a transient constraint occurred, which corresponds to the time of elongation of the affected organ length. This method was described in my PhD thesis (Lafarge, 1998). This applies particularly well with the pattern of internode lengths as internodes, to the difference of blades and sheaths, do not senesce and are still intact at maturity. One measurement at maturity is sufficient to reconstitute the history of transient stress occurrence during the crop cycle. In my mind, this resembles to the technique of sampling ice cores from the Antarctica continent and reconstituting the climate history by analyzing the composition of the air molecules trapped inside the cores.

C - Competition between sinks within the plant and phenotypic plasticity

1 - Dynamics of leaf appearance

Leaf emergence with time is the relevant marker that allows to position in time the overall coordinating framework of the growth phases of the plant: (i) it is strongly coordinated with the start and end of the elongation phases of each shoot organ, (ii) it determines the potential tillering dynamics and the rhythm of emergence of the vegetative sinks of the plant, and (iii) it is a non-invasive measurement. In this way, leaf emergence is the key dynamics often used as a reference for genetic diversity and G x E analyses, and as a timer within crop models.

Leaf emergence (case of a hybrid sorghum variety) is linear with thermal time in the case of a main tiller producing a total of 16 leaves and similar between the main tiller and the primary tillers (Lafarge et al, 2002). Emergence of the flag leaves of the primary tillers is just delayed by about two phyllochrons (the time between the emergence of two consecutive leaves) compared to that of the main tiller. Similarly, in the case of rice, leaf emergence is similar between the main tiller, one primary and one secondary tillers (case of the variety IR64, Figure 6). Leaf emergence with thermal time can be described in rice with two consecutive linear relationships for each of the three culms, the slope of the early one being higher than that of the late one. For each relationship, the slopes are similar for the three culms, except the early one of the secondary tiller that is higher than those of the main and primary tillers. The break in slope is concomitant with the three culms and occurs at the emergence of leaf 12 of the main culm. This break in slope may correspond to the start in internode elongation of

the culm but is probably not the consequence of any competition for resources as leaf elongation rate of the phytomers at positions lower and upper than position 12 was similar. The explanation for me is rather morphological: due to the increase in length of the sheaths of the upper phytomers, the whorl (the distance one leaf needs to cover before emerging out) gets longer and so the duration during which the leaf needs to grow within the whorl gets longer and the emergence is delayed. This break in slope was not reported with hybrid sorghum, but there was a tendency for it in the case of the variety E35-1 grown in Western Africa (Lafarge and Tardieu, 2002). In other studies using highly photosensitive sorghum lines, this break in slope was confirmed also in sorghum.

2 - Tillering

2.1. Tillering dynamics

Case of rice

Most of the following data I am commenting here were obtained from high-yielding *indica* genotypes selected by the irrigated breeding program of IRRI. Considering this program was fully conducted in one environment that is the IRRI farm under transplanting conditions, although during both the wet and dry seasons, the expected variability amongst the high-yielding genotypes was not high. In order to include much contrast between the genotypes under study, I have decided to focus on a detailed comparative analysis of the best hybrids over the best inbreds: performance of hybrids is widely reported as being 15-20% higher than that of inbreds, and this difference has set up the basis from which key traits supporting the higher yield were analyzed and reported at the whole plant level.

High rate of leaf production on the main tiller, and so of axillary buds, was observed as long as high-yielding varieties were concerned. This is the direct consequence of breeders' main objective of a quick canopy closure in order to maximize early biomass production but also to compete against weeds at early stage. This rate was similar across the range of genotypes under study, whatever an inbred or a hybrid that was probably facilitated by the similar crop duration of these genotypes. The rate of tiller emergence was also similar across the same genotypes, and namely was not different between inbreds and hybrids (Bueno et al, 2009). This dynamics can be represented by the succession of an exponential function until about 200 tillers m^{-2}, then a linear function thereafter until time of maximal tillering. Recent breeding programs have targeted to reduce tiller death by making most of the initiated tillers productive as was the breeding for the New Plant Type (NPT) at IRRI. The program was indeed successful in developing modern genotypes with high tiller efficiency and larger panicle size, but was a failure in terms of performance: it has been extensively published that grain yield of NPT was significantly reduced. Among other reasons that I have not analyzed in details, I have noticed that the reduction in maximum tiller number of NPT was due to a lower rate of tiller emergence than an earlier time for cessation of tillering (Figure 7). The essential contribution of tiller emergence to grain yield was well illustrated with the issue of the nursery management. Traditionally before transplanting, rice seedlings are grown within nurseries under high seed density (3000 seeds m^{-2}) until they are transplanted in the main field at the stage of about 5-6 emerged leaves on the main tiller (which is about 20 to 25 days after sowing). Considering the long stay in the nursery under high plant competition for access to light, tillering did not start within the nursery, but only when the seedlings were transplanted in the main field at 25 pl m^{-2}. The longer the stay in the nursery, the more delayed the tiller emergence started. The delay in tiller emergence from 7 to 14 and 21 days after sowing had significant impact on biomass production and grain yield, although panicle number per plant at

maturity was similar (Pasuquin et al, 2008). These behaviors were similar for three contrasted high-yielding genotypes under study. By extending the range of conditions with a transplanting range from 7 to 35 days after sowing, the delay in tillering and in biomass accumulation per plant was even wider: it was of about 30 days of delay in tiller emergence with the maximum tiller number per plant ranging from 13 to 23 (Figure 8). This illustrates how any transient stress conditions affecting tiller emergence can affect crop performance. In the same way, even when transplanting was done early, the first tiller to emerge in the main field was in most cases that initiated from the axillary bud of phytomer 3 of the main tiller. This observation was largely valid over years. Considering that each phytomer has an axillary bud and that each bud is potentially able to initiate a tiller, the absence of tiller initiation from axillary bud 1 and 2 raises the question of the nursery effect even in the case of transplanting young seedlings. This is confirmed by my regular observation of emergence of tillers from buds 1 and 2 when the plants are grown in pots in the greenhouse. In contrast, when looking at a diversity panel of 184 tropical japonica genotypes grown in a greenhouse in Brazil, I was able to observe many plants growing a tiller 1 and even 9 of them growing a tiller from the prophyll (the immature leaf produced before leaf 1) of the main tiller. It is noteworthy that the size of the leaf 1 and 2 of tropical japonica genotypes is far larger than that of the same leaves in indica genotypes. In the case of indica sub-specie, where observations for hybrids and inbreds in the field were similar, the earliest initiated tiller as tiller 3 may represent the best the breeding programs for high yield could achieve under transplanting conditions.

Cessation of tiller production occurred earlier with hybrids compared to inbreds, at lower maximum tiller number since the emergence rate was similar (Bueno and Lafarge, 2009). Because of profuse tiller production in a rice canopy, high rate of tiller death was also observed in such canopies that could reach around 50%. Indeed, it has been reported from the comparison between hybrids and inbreds that an efficient but productive genotype with lower maximum tiller number and higher tillering efficiency would maintain high rate of tiller emergence while stopping tiller initiation earlier. Higher grain yield of hybrids could then be due to (i) higher tillering efficiency or (ii) larger reserves accumulation in the plant. Already, higher tillering efficiency of NPT did not translate into higher yields, and this was associated with a strong delay in tiller emergence (Figure 7) and so in biomass accumulation. In addition, as reported from trials evaluating performances of several contrasted high-yielding genotypes, grain yield was not correlated with tiller efficiency varying in the range from 0.5 to 0.8 in the dry season and from 0.4 to 0.8 in the wet season (Figure 9). This was also the case for biomass at flowering and harvest index. It seems that a decent rate of tiller senescence does not have any detrimental impact on the crop performance.

The rate of tiller efficiency is then higher with hybrids than with inbreds because of a lower maximum tiller number but similar panicle number at maturity. In fact, because of the earlier cessation, hybrids store some C resources when inbreds are still investing C resources into new tillers that will eventually die. This better sink regulation of hybrids can also be observed at later stages. I was able to evaluate that stem vigor of hybrids at flowering time, remobilization ability at early grain filling and the rate of spikelet filling were all higher than the same process of inbreds (Lafarge and Bueno, 2009). The higher sink regulation of hybrid rice over inbred lines was confirmed when considering additional sites and seasons and genotypes (Bueno et al, 2010). At the plant level, the better sink regulation of hybrids was one key explaining the higher yield reported over best inbreds. At each single process level, this represented small differences between the two types of genotypes which was not easy to detect, but at the whole cycle level, the addition of small differences made the difference greater and that

contributed greatly to yield performance differences reported in the field at maturity. Another source of hybrid superiority was the higher ability of hybrids to accumulate biomass during each of the three developmental phases, the vegetative, reproductive and ripening phases.

The better sink regulation revealed with hybrids from tillering stage inducing higher final yield was also the key process generating the larger panicle size of qTSN4 rice genotypes. These genotypes carrying a QTL considered by the breeders to have a direct effect on the increase of panicle size was in fact acting at earlier stage on tillering dynamics, and through a cascade of events eventually on panicle size: an earlier cessation of tiller emergence was identified with these genotypes which generated higher main stem growth rate (negative correlation between main stem growth rate and tillering rate) and main stem panicle dry weight (positive correlation between panicle dry weight and stem growth rate) (Adriani et al, 2016a). The higher panicle size was then associated with an earlier cessation of tillering, a stronger above-ground biomass of the tiller, larger area of the top leaves and larger cross-section of the upper nodes. This confirms the importance of the earlier traits in the determination of yield components.

Case of sorghum

Tiller emergence is far lower in sorghum than in rice. In the case of sorghum grown in Western African conditions, as I could observed it during my PhD work and some field trips, there may be 1 or 2 primary tillers in addition to the main tiller, but not more. During my postdoc, I have worked with a sorghum hybrid that possessed a high ability of tillering. Tiller number raised up to 6 per plant, although all the tillers were primary, under plant density as low as 2 pl m^{-2}. Some buds of phytomers 1 and 6, most of the buds of phytomers 2 and 5, and all buds of phytomers 3 and 4, initiated a tiller (Lafarge et al, 2002). This dynamic was linear and well aligned to the increase in leaf ligule number on the main tiller (Lafarge and Hammer, 2002a). No secondary tillers were produced. Tiller emergence varied significantly under the range of plant densities from 2 to 16 pl m^{-2}, where 1 or at the highest 2 tillers per plant, that eventually died, were produced under 16 pl m^{-2}.

Cessation of tiller emergence, interestingly, occurred at a leaf area index (LAI) close to 1 in the conditions of the experiment, whatever the plant density, 2, 4, 8 or 16 pl m^{-2} (Lafarge and Hammer, 2002a). The rate of tiller senescence was also dependent on a leaf area component, as linearly related to the ratio of realized to potential leaf area growth during the period of tiller senescence (Lafarge and Hammer, 2002a). The senescing tillers were the smallest and less vigorous of the plant. The direct relationship of the time of cessation in tiller emergence and of the rate of tiller senescence with a demand component in leaf area growth within the plant supports the fact that the control in tiller production is driven by an internal plant trophic status: this may stop when the C supply:demand ratio falls below a certain threshold. However, it has not been investigated if this threshold varies with genetic diversity, and if it is higher than 1, meaning the plant would be sensitive to light signals within the canopy ahead of C limitation to prevent high tiller senescence, or lower than 1 which may favor tiller emergence to the detriment of tiller fertility, and so induce higher tiller senescence.

The weight of tiller senescence was evaluated when comparing a sorghum crop grown at 16 pl m^{-2} with the same crop grown in the same conditions but with a systematic removal of any tiller of the plant as soon as it emerged. In the case of the undisturbed crop, 1 to 2 tillers emerged per plant but incidentally senesced and died before maturity. At term, under the same plant density of 16 pl m^{-2}, only uniculm

plants were reported at maturity but through tiller senescence in one case (undisturbed crop) and systematic tiller removal in the other case. The significant difference in grain yield measured at maturity, 9.5 t ha^{-1} for the tiller removal case and 11.5 t ha^{-1} for the undisturbed case (Lafarge et al, 2002), highlighted that tiller senescence has a significant cost on the overall production and is clearly detrimental for grain yield.

2.2. Tiller hierarchy within the plant

Case of sorghum

The same tiller hierarchy applied across the large range of plant density for the emergence rate of each individual tiller, their vigor with time, their fertility rate, their grain number, and their contribution to yield (Lafarge et al, 2002). Individual tiller performance of tillers 3 and 4 was higher than that of tillers 2 and 5, that was higher than that of tillers 1 and 6. Indeed, individual tiller vigor and productivity increased with tiller age up to tiller 3 and decreased with tiller age from tiller 4 onwards. The fate of individual tillers seemed to be clearly dependent on the trophic status of their subtending leaf at the time of its emergence. The tillers that emerge at the highest rate were the highest contributors to yield (tillers 3 and 4), and were those with a subtending leaf larger than that of tillers 1 and 2, and most probably less subjected to internal competition for C resources than that of tillers 5 and 6 (more tillers are demanding for resources simultaneously at time of tiller 5 and 6 emergence). Surprisingly, the vigor of the main tiller was not higher than that of tillers 3 and 4.

Case of rice

The hierarchy across tillers indicated higher performance of the colonies developed from tiller 3 and 4: they are the highest in terms of number of initiated and productive tillers and tiller fertility rate, and number of filled grains (Figure 10). The superiority over colonies of tiller 1 and 2 was due to the absence of tillers 1 and 2. This behavior is confirmed by many observations I did in the field where initiation of tillers 1 and 2 did not occur and tiller 3 was often the first tiller to emerge for a large range of varieties. The superiority over colonies of tiller 5 onwards increased with colony number and was explained by the lower number of initiated tillers and higher rate of unproductive tillers among the initiated tillers (Figure 10). For each colony, the adjustment of tiller number was the fact of the secondary tillers while the primary tillers were always those with the highest productivity within a colony. The performance of the main tiller was higher than that of any succeeding tillers, in terms of number of filled grains per productive tillers (Figure 11).

2.3. Comparison between sorghum and rice

The dynamics of tiller emergence for both species was related to that of main tiller leaf emergence, either as a linear relationship (sorghum) or an exponential-type relationship (rice) nicely simulated with a Fibonacci series (Clerget et al, 2016). Also, the hierarchy across tillers within both species was similar for the cases evaluated in these studies: the most vigorous primary tillers (sorghum) or tiller colonies (rice) are 3 and 4. Primary tillers or tiller colonies 1 and 2 were strongly affected by the absence of the corresponding primary tiller which may be due to the small size of its subtending leaf or the unfavorable ratio of C supply:demand in the case of young seedlings. Primary tillers or tiller colonies 5 onwards were affected because of their delay in development and lower vigor at a stage when the ratio of C supply:demand at the whole plant level was unfavorable due to the increasing number of growing structures. These similarities between rice and sorghum were reported although the tillering production in rice, that may include the development of tertiary tillers, was far stronger

than that of sorghum for which only primary tillers emerged. The control of cessation in tillering in sorghum was nicely related to a LAI value. This tends to indicate that tillering production, even if is eventually driven by the internal plant trophic status, may be sensitive to the quality of light signals within the canopy which are known to vary with canopy coverage. The change in red/far-red ratio within the canopy has already been reported as an environmental factor involved in the control of tillering. In rice, I was not able so far to identify stable relationships considering the control of cessation in tillering. Although a response to the internal trophic status of the plant is most probably involved and can be implemented in crop models with a parameter representing the trophic status, some further research should be initiated on this topic.

An interesting contrast between both species is the weight of tiller senescence: as it was measured detrimental for sorghum, with significant differences in yield between an undisturbed and a tiller-free canopy, in rice it did not have any impact on grain yield as long as the plant density was reasonable (around 25 pl m^{-2}). In rice, as being smaller than the productive tillers, non-productive tillers may not compete much with taller tillers for access to resources. As carrying several green leaves at time of flowering, they were able to intercept light that was not intercepted by productive tillers and to use this resource at least for their own respiratory needs. Where in sorghum the investment in biomass per non-productive tiller appeared as a waste of energy, the non-productive tillers in rice, however, may play a key role in yield potential by intercepting light non captured by productive tillers and remobilizing C and N resources to productive tillers during the process of senescence. The cost of tiller senescence in sorghum may explain why selection has come to uniculm or low-tillering varieties in most environmental conditions whereas breeding programs for high-yielding rice varieties developed germplasm characterized with high-tillering ability and significant rate of tiller senescence. One hypothesis that may explain the difference in the impact of tiller senescence between sorghum and rice is the likely maintenance in rice of vascular connections at the base of the plant between tillers while such connections may be dismantled early in sorghum leading to autonomous tillers. Obviously, profuse tiller production as it may be observed under high density sowing under direct-seeding conditions (up to 100 kg seeds ha^{-1}) would be detrimental for grain yield as the rate in tiller senescence may then reach values significantly higher than 50%, close to 70%. Another hypothesis here is that the rice plant would need to reach a certain stage before being sensitive to the signals involved in the control of tillering, in the same way as plant is sensitive to photoperiod only after the end of the Basic Vegetative Phase (BVP), which has already been widely published. In the case of conventional plant densities like 100 pl m^{-2} under direct-seeding, dynamics of tiller density is so advanced, compared to conventional transplanting conditions at 25 pl m^{-2}, that the critical tiller density for cessation of tillering may be reached before the plant juvenile phase is over. This gives credit to the control of tillering via the involvement of a signal that may be immature in case the plant is too young.

2.4. Plasticity of tillering and SLA, and biomass partitioning, in response to growing conditions

Tillering plasticity

Tiller production is very plastic and appears as one of the first component traits to be adjusted to the growing conditions. This is quite obvious in response to contrasted plant densities in the field like a range of 2 to 16 pl m^{-2} in sorghum where it varied from 0 to 5 with a high-tillering sorghum hybrid. Thanks to the tillering plasticity, even though it is quite limited in sorghum, grain yield of 10.5 t ha^{-1} was similar for densities of 4 and 8 pl m^{-2} (Lafarge et al, 2002). It concerned a difference of 1 to 2 tillers per plant. In contrast, the limit of the tillering plasticity in sorghum is reported at a lower density, 2 pl

m^{-2}, where tillering, in the case of this variety, could not compensate the low plant density so that grain yield, 9 t ha^{-1}, was lower than that at higher densities. In rice, the ability to compensate through tillering the variability in growing conditions is high. In response to 70% shading in the field, tiller emergence was stopped the time of lower radiation, and resumed back to its formal rate as soon as light conditions were back to normal (Lafarge et al, 2010). Also, in response to the removal of primary tillers 3 and 4 in rice, emergence of secondary tillers was about double compared to the undisturbed plot for each of the colonies 5 (from 5 to 10), 6 (from 4 to 8), 7 (from 2 to 4) and 8, and so was the number of productive tillers from colonies 5 and 6 (Figure 12). The ability of the plant to initiate a tiller from the bud of any phytomer was even confirmed with isolated sorghum plants of which any emerged tillers were systematically removed as soon as they appeared: during grain filling, some tillers (just composed of a peduncle and a head) emerged from the axillary bud of the flag leaf phytomer to provide an additional sink to the surplus of C materials unused due to the artificial reduction of the demand. This late emergence of extra panicles happens also in response to the occurrence of diseases or extreme climate conditions that would make some of the original panicles sterile or unable to import C compounds. Tillering plasticity is well illustrated in response to distinct nursery management: when seedling age at transplanting varying from 7 to 21 days after sowing, tillering was reported to start few days after transplanting, which did not correspond to the same seedling age and developmental stage (Pasuquin et al, 2008). Also, when seedlings were grown at 500 seeds m^{-2} in the nursery but for a long duration of 35 days, tillering even started within the nursery 15 days after sowing, stopped in response to the high seedling competition within the nursery, and resumed soon after transplanting in the main field (Figure 13).

SLA plasticity

To the difference of the high visibility of tillering plasticity in situ, the plasticity of specific leaf area (SLA, the area of a leaf unit divided by its biomass, here considered at the whole plant level), can be questioned. Indeed, the classical dynamics of SLA, decreasing with time from early stage, quite rapidly until mid-reproductive phase, then slower afterwards, appeared to be well buffered with time in response to the increase in plant density from 2 to 16 pl m^{-2} in sorghum, where its maximal increase was about 20 cm^2 g^{-1} (Lafarge and Hammer, 2002b). The role of buffer of SLA in the course of plant growth across diverse growing conditions indicates that SLA is not a main component of plant plasticity to the opposite of tillering. Even when systematic tiller removal reduced considerably the plant demand in sorghum, the reduction in SLA at the whole plant level was only 30 cm^2 g^{-1} from that of the undisturbed plant grown at the same density (Lafarge and Hammer, 2002b). The difference between the value of undisturbed plants grown at high density (16 pl m^{-2}) and that of plants with systematic tiller removal grown at low density (2 pl m^{-2}) indicates probably the highest range of variation of SLA in the course of plant growth, and was 50 cm^2 g^{-1} with the genotype under study. This also provides threshold values of SLA, like 110 and 160 cm^2 g^{-1} at flowering, which may be interesting for crop modeling purposes.

In contrast, in response to sudden changes in growing conditions, the variation in SLA is quick, wider and sustained for the whole period of stress. (i) In the rice field where 70% shading was imposed to the crop from 400 °C days after sowing, SLA suddenly increased by 50 cm^2 g^{-1}, from 250 to 300 cm^2 g^{-1} (Lafarge et al, 2010). It was maintained high during the time of shading, 50 °C days, after which it decreased back to the value of the non-shaded plants. At the same time, concentration of soluble sucrose and starch in leaves and sheaths were five times lower under shading than under full radiation. Tillering was then maintained for a while thanks to the release of C metabolites from the leaves until

it was affected because of the lack in C resources. In the case of plants subjected to shading until flowering, the value of SLA was maintained 50 cm^2 g^{-1} above that of the undisturbed plants during the whole period of shading (Lafarge et al, 2010). This value shall correspond to the upper value this variable can reach at crop level and highlight that leaves during vegetative phase play a role of transient storage of reserves that can be mobilized any time. (ii) Right after transplanting, probably as a quick reaction to the stress of uprooting and replanting, SLA dropped for 2-4 days to values of about 50 cm^2 g^{-1} lower than expected values of non-transplanted plants (Pasuquin et al, 2008). In fact, this abrupt and quick change in SLA right after transplanting may be the best representation of the 'transplanting shock', with C assimilates being first stored in leaves as a quick 'protective' response to uprooting before the seedlings grow normally. These observations indeed highlight the high sensitivity of SLA to sudden changes in growing conditions as a way to play a role of daily buffer to compensate for variable climate conditions either by storing or releasing carbohydrates and to sustain plant growth despite the stress occurrence. They also indicate the 'priority' of SLA to get back to its 'buffer' value as soon as possible, most probably to be ready to respond to any other occurrence of additional stresses if any.

Panicle plasticity

The plasticity of the rice panicle was not as pronounced as that of the number of panicles as observed in the response of removal of primary tillers 3 and 4. Even if the 50% increase in the number of productive tillers of colonies 5 onwards compensate partly the tiller removal, the average panicles of the same colonies were also larger than those of undisturbed plants with number of filled grains higher by about 35% (Figure 16). In contrast, grain size (1000 grain dry weight) appeared as a heritable trait that did not vary between tillering treatments and even between colonies. In terms of yield components, the traits the most plastic seem to be the number of productive tillers first (which is also the first component trait that is determined in the course of yield establishment), the panicle size second, which is also the second component trait that is determined in time.

All the panicle traits were affected in response to shading, i.e. the rachis, primary and secondary branch length, and the primary and secondary branch number, and the spikelet number, while studying NILs carrying a QTL for larger panicle and their parents (Adriani et al, 2016b). Branch number, mostly secondary branch number, rather than branch length, was the trait the most affected. This was also reported under higher plant density in the field, although this was not observed on all the genotypes under study. Interestingly, the ratio of spikelet number over total branch length per panicle was conserved across many variations of both variables, indicating that the panicle shape was maintained across conditions and that branch number was the adjustment variable. The role of secondary branch number appeared essential in driving panicle size, with this trait being the most sensitive panicle trait to light conditions. This resembles to the response of tillering to shading with tiller number, rather than stem elongation, being the most affected trait (Lafarge et al, 2010).

Discussion

Plant plasticity is essential in the adaptation to fluctuating conditions, where SLA in rice and sorghum appears as the first morphological trait involved: although its range of variation is quite narrow, it can adjust rapidly in storing or remobilizing carbohydrates and so overcoming the sudden occurrence of a stressing period. In case of a 1 to 2-day transient stress, the brief change in SLA might be enough to face the adverse conditions. Even under favorable growing environments, transient stressing periods can occur like fluctuating climate conditions as with variable daily radiation or soil water availability (under the AWD technology), or disturbing cultural practices like transplanting. The SLA can go back to

its expected values as soon as the stressing period is over. In case of a prolonged stress, tiller dynamics in rice is easily adjusted to address changes in growing conditions. Tiller production is reduced in case of a reduction in available assimilates like under shading or high plant density, or if water reserve would become short. As soon as conditions come back to normal, tiller production is back to normal. The plasticity in tiller dynamics is also expressed as an extension of the tillering period if tiller production was substantially delayed during crop growth (as a response of an extended stay of the seedling in the nursery). In sorghum, because of poor tillering ability and the probably high biomass investment per tiller, organ size like individual leaf area and internode length may be the next adjustable morphological traits after SLA. Leaf emergence rate is not appreciably affected in rice while it is more sensitive in sorghum.

D - Conclusion

Early and quick tiller emergence in rice was reported in my work as essential to achieve high yield: it was present in the highest-yielding varieties, which includes hybrids and improved inbreds, and was expressed similarly between these genotypes, indicating that crop improvement was successful and probably reached an upper limit in tillering ability at early stage. In their goal of increasing tiller efficiency, breeding programs then developed a New Plant Type that indeed was characterized with a higher ratio of productive tillers, but this was unfortunately associated with a delayed in tiller emergence from early stage. The inferior grain yield measured with NPT compared to that of reference varieties reinforced the importance of early and quick tiller emergence in achieving high performance. Indeed, any stress affecting tiller emergence would affect grain yield. (i) This is the case of high seed density established within rice nurseries before transplanting: a prolonged stay in the nursery delays the emergence of the first tillers and the time when maximum tiller number per plant was reached, and affected significantly grain yield, despite similar panicle number produced at maturity. Even a short stay in the nursery most probably prevented from the emergence of tillers from axillary buds 1 and 2, and this may had an effect on grain yield although this was observed with all high-yielding varieties. (ii) This is also the case of transient shading that delayed tillering during the time of shading even though the plasticity in SLA, and its maintenance at its upper value, contributed to the maintenance of tillering emergence before it was affected. In addition to the delay in tillering, there was also an over-reaction of the plant that tended to accumulate reserves, at least with the main tiller, after the removal of shading, probably as a 'memory' response in case another stressing period would occur.

High sink regulation was revealed a key overall process supporting high yield when comparing growth behavior of hybrids vs. improved inbreds, and also as a good candidate for crop improvement. Sink regulation is considered here as the plant ability to modify the priority between its sinks relative to crop stage and growth conditions to make biomass partitioning as much efficient as possible. In this way, a comparative analysis of biomass partitioning between hybrids and inbreds reported that sink regulation was consistently higher with hybrids: considering that tiller emergence was similar as stated in the previous paragraph, the cessation of tiller emergence was earlier with hybrids, and the biomass storage within stems and the remobilization of reserves from the stem to the panicle was superior. Instead of pointing out a specific process, this is rather the addition of each single process involved in the better sink regulation that makes a significant differences in crop performance at maturity. The earlier cessation of tiller emergence was also the characteristic of a qTSN4 introgressed line. In fact, the larger panicle size of the main tiller of this line was not the consequence of a direct effect of the

QTL, as initially assumed by breeders, but the result of its higher growth rate (and vigor) induced by the earlier plant cessation of tiller emergence. The impact of the higher early vigor of a tiller on its own productivity was systematically supporting the hierarchy between tillers: the tillers with the highest growth rates were the ones with the largest panicles, which was the case with rice but also with sorghum. In this way, by favoring growth rate of individual tillers rather than emergence of additional tillers, sink regulation at plant level induced higher grain yield.

It is noteworthy that what is commonly mentioned as a 'transplanting shock' to explain the delay in plant growth in the main field after transplanting is in fact a stress due to the extended stay under high plant competition within the nursery: the dynamics of leaf number on the main tiller has not been significantly affected by transplanting *per se*, as it was the same before and after transplanting, but it has been affected by competition within the nursery as it was slower as seed density increased (Figure 15). Tillering was delayed when the seedling was grown too long in the nursery, but as soon as transplanting was done, tillering was rapid and compensated the delay in transplanting in terms of tiller number but not in terms of plant biomass.

Overall, plant plasticity is governed by the changes in priority in-between sinks that represents sink regulation. In favorable conditions, plasticity in SLA first, plasticity in tillering second, are the early plant response to transient climate fluctuations. Also, genotype superiority, as in the case of hybrids over inbreds, is supported by a more efficient sink regulation. It is, however, not straight forward to identify whether sink strength or source availability governs crop performance and grain yield. In one hand, if sink strength is limited, source acquisition may then be downregulated. If sink strength is stronger, source acquisition is stimulated. On the other hand, if source acquisition is limited or increased, sink will be developed accordingly. One may wonder whether the answer to this question is crucial as source acquisition and sink strength seem to be tightly inter-related: if the source acquisition is increased, sink strength shall follow, and vice versa. The grain filling ratio at maturity could serve as an adjustment variable of the growing conditions during grain filling on the basis of the balance between source acquisition ability and sink size established at flowering. An increase either of source acquisition or of sink strength should lead to higher yield, however, such achievements in crop improvement are not that simple: a good example is the compensation phenomena, with the increase in panicle size often associated with a reduction in panicle number in today's genotypes that are already characterized with a large sink size. In contrast, one approach that seems to be relevant on the basis of the data described here is the improvement in sink regulation and the increase in partitioning efficiency. This shall reflect the timing of sink activities within the plant, with such processes as tillering which was analyzed here, remobilization through senescence, distribution of filling in-between spikelets within the panicle. This will be the main focus of the project I will describe in this manuscript.

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II - Plant adaptation to climate change

Because of higher recurrence of extreme high-temperature events and a projected global average surface temperature increase of 1.5 to 4.8 °C by 2100 (Battisti and Naylor, 2009; IPCC, 2014), yield decrease in the 2nd half of the century is predicted to be even stronger in the tropics than in the temperate areas (Challinor et al, 2014). Considering also a simulated increase in annual mean of maximum temperature during the period 1990-2050 of 0.5 to 1.0 °C in the Northern and Central part of South-East Asia, and of 1.0 to 1.5 °C in the southern part (Chotamonsak et al, 2011), the analysis of the genetic diversity and its tolerance to heat and the improvement of crop models to better take into account the response of physiological processes to higher temperature are becoming burning issues to address.

Some adaptation strategies to heat in rice have been recently analyzed and described by Julia and Dingkuhn (2012, 2013). As an escape strategy, plants have already the ability to adjust the time of the day of anthesis depending on their sensitivity to climate conditions during the 7-days period preceding anthesis (Julia and Dingkuhn, 2012): anthesis is advanced earlier in the morning if conditions during the seven preceding days are hot and humid, allowing the plants to escape the hottest time of the day. As an avoidance strategy, in dry air environments, the transpirational cooling ability of the plant can lower panicle temperature by up to 10°C compared to air temperature and so stabilize spikelet fertility by maintaining panicle temperature below the critical threshold (Matsui et al, 2007; Julia and Dingkuhn, 2013). Sterility is, however, still a major concern in rice cultivation areas despite the occurrence of escape and avoidance strategies because most of the concerned regions are characterized with humid conditions, limiting the incidence of transpirational cooling, then panicle temperature reduction (Tian et al, 2010; Julia and Dingkuhn, 2013).

Better taking into account the plant response to temperature into crop models implies to confront through trials the function driving plant response to temperature, and to modify it if necessary. In the case of rice, mostly grown in tropical and subtropical regions, the increase in temperature goes with systematic yield reduction even in conditions when day temperature was not detrimental to spikelet fertility. In this way, Peng et al. (2004) reported a stronger correlation of the reduction in yield with the increase in night temperature than with the reduction in radiation over a series of 12 dry season crops in the tropics. This tends to indicate that the sensitivity of respiration to night temperature is strongly increased at higher temperature. It is then needed to evaluate whether any variation of respiration would have a significant impact on overall biomass, and whether the actual rule for the respiration sensitivity to temperature (Q = 2) is still valid.

A - Revealing genotypic diversity and improving models and in response to high temperature

A decline in agricultural productivity is projected for low-latitude agricultural systems due to detrimental thermal conditions and more frequent extreme weather-related events. Rising temperatures will lower production by limiting the length of the growing season and exerting direct negative effects on resource capture (stomatal closure) and growth processes (reduced elongation

rate). Both night and day temperature are concerned although it has been reported that increase in night temperature will be higher and will have greater negative impacts.

The tolerance of spikelet fertility to heat

The detrimental effect of high day temperature on spikelet fertility and its impact on grain yield is not anymore a hypothesis. Beyond the understanding of the variation of time of the day of anthesis and of the change in panicle temperature in response to climate conditions (Lafarge et al, 2015, extracted from Julia and Dingkuhn, 2013 and 2014), the search for relevant QTLs providing tolerance of spikelet fertility to heat is becoming a priority. In the absence of mapping populations devoted to this issue, this work was conducted on a diversity panel of 167 varieties that has the advantage of exploiting extreme allelic richness due to millions of historical recombination and genetic markers in low linkage disequilibrium. Small genetic regions of interest with high resolution can then be revealed through association mapping even though this type of analysis requires a large number of SNPs that are now widely available, in that case more than 13 000 markers were used with an average density of one marker per 29 kb and with the r^2 estimate of LD averaging 0.51 for marker pairs whose distance was below 25 kb (Lafarge et al, 2017, in press). Based on the results from three association analysis methods, a total of 22 SNPs significantly associated with spikelet sterility were revealed under at least two methods, with 14 were independent loci. Among these 14 loci, eight colocalised with QTLs reported in the literature for tolerance to high temperature during the reproductive stage. This GWAS experiment allowed (i) to narrow-down the position of these eight QTLs previously detected in bi-parental crosses and (ii) to detect six new QTLs (Lafarge et al, 2017, in press). Haplotypes analysis at the vicinity of individual significant loci confirmed that favorable alleles for heat tolerance during anthesis are not confined to a few accessions but are rather widespread across genetic groups.

The power of detection of this analysis is partly due to its fine phenotyping: (i) the exposure of plants to 38°C at time of anthesis was only done from 8am to 2pm and for 6 consecutive days to minimize the high temperature effect on other processes, (ii) the panicles that flowered fully under 38°C, and the same panicles of the control plants, were tagged and only those panicles were analyzed for tolerance of spikelet sterility to heat, and (iii) the top half part of the relevant panicles was finally analyzed to avoid taking into account unfilled spikelets due to lack of resources within the bottom half part of the panicle. While phenotyping is by far the time-consuming step of association analyses, it is also critical respective of the rigor of the protocol that is established. Phenotyping often requires a good understanding (i) of the adaptation strategies at the whole-plant level to break-down complex traits into component traits and to consider trade-offs between traits, (ii) of the appropriate growing conditions under which the plant behavior should be characterized, and (iii) of the time when and the way how to quantify component traits. Taking these requirements into account, phenotyping protocols shall be reliable only if they are validated by crop physiologists. This would avoid waste of time and money associated with crappy protocols.

The effect of night temperature on respiration

Considering negative correlations published between historical grain yield and night temperature, respiration appeared to me as one key process possibly involved in the reduction in grain yield over time through greater consumption of carbohydrates. While no escape or avoidance pathway can address the effect of high night temperature on respiration as it occurs at night when the plant cooling system is minimal and mostly at any time during plant cycle so that the plant cannot really escape it,

tolerance is seen as a major option. Suggesting this issue to colleagues from Bayer CropScience interested in contributing to some dedicated research in the context of climate change, they agreed to fund a PhD program that I co-supervised. The objective was to quantify to which context respiration is affected by the increase in night temperature and if this likely change may have a significant impact on grain yield. To address this issue, it was decided to evaluate the response of a range of contrasted genotypes to appreciable increase in night temperature of 4-5°C in greenhouses and growth chambers, but also to increase in night temperature in the field even though this one was not higher than 2°C. This latter case was made possible thanks to a new T-FACE facility that was just established at IRRI and that heated an area of 4.5 m^2 of plants with infrared thermometers (Peraudeau et al, 2015a).

Night respiration was confirmed to be increased by higher night temperature, even by a small increase of 2°C in the field, and by 4-5°C increase in the greenhouse and growth chamber (Peraudeau et al, 2015a). This increase, however, was not associated with a significant decrease in biomass at flowering and maturity, neither with a significant reduction in grain yield. To confirm this observation, the cost in carbohydrates of respiration was evaluated over the crop cycle as 17 to 20% in the field, and 8 to 18% in the greenhouse, of the potential shoot dry matter at maturity (that calculated considering no loss from respiration and senescence). In case of higher temperature set during the whole crop cycle, the additional loss of carbohydrates through respiration was only 1 to 7% of the potential shoot dry matter, which was not associated with significant reduction in plant biomass (Peraudeau et al, 2015a). The non-significant contribution to the reduction in crop biomass of the increase in respiration in response to higher night temperature opens some new hypotheses to the likely grain yield reduction under higher night temperature. One is that higher day temperature or change in radiation, rather than higher night temperature, would be the climate factor involved in the response. Others shall consider biomass partitioning, tiller and leaf senescence, biochemical processes.

The temperature effect on respiration within crop models

Mitochondrial respiration is commonly divided in two functional components. (i) Maintenance respiration is associated with all biochemical reactions required to maintain existing biomass. The rate of this respiration component would double when ambient temperature increase by 10°C (Q10=2). (ii) Growth respiration is associated with all processes involved in establishment of new biomass. This respiration component is driven by carbohydrate supply (the photosynthesis rate), and by plant demand. The main challenges of this study were to distinguish the measurements of maintenance from growth respiration and the acclimated from the non-acclimated response. The maintenance respiration was evaluated during the night following a 12h-day period under full darkness to get the plants close to C starvation. While the increase of night respiration with temperature rising from 21 to 31°C was 2.4-fold without acclimation, it was only between 1.2 and 1.7-fold with acclimation (Peraudeau et al, 2015b). In the same way, the maintenance respiration, which was estimated by assimilate starvation at 34% of the night respiration, increased by a factor of 1.49 when temperature rose from 21 to 31°C. Considering that the respiration response within crop models has to be the acclimated one (the one corresponding to natural conditions), these figures are lower than the common assumption of the Q10=2 rule that overestimates the effect of increasing night temperature on respiration in acclimated conditions. A Q10=1.5 rule seems closer to the reality to account for respiration changes with temperature into crop models where the estimation of canopy temperature is essential to predict spikelet sterility.

B - The combined effect of elevated temperature and [CO_2]

Elevated [CO_2] stimulates photosynthesis, particularly in C3 crops for which Rubisco is not CO_2 saturated at current [CO_2], and inhibits photorespiration, and so increases carbon supply to physiological processes involved in plant organ expansion. The response to elevated [CO_2], however, is often down-regulated as the average stimulation is being reported to be just a part of what is expected: while rising [CO_2] provides the opportunity to increase the productivity of C3 crops, average yield stimulation observed to date is well below potential gains. Also, recent cultivars are not responding better to elevated [CO_2] than older ones although they have been bred under higher [CO_2]. Indeed, much gain in crop production is expected from elevated [CO_2]. The benefit of elevated [CO_2] was confirmed 28.2°C of tissue temperature both on vegetative growth and seed yield in a study conducted within growth chambers (Madan et al, 2012). And this was the case for three genotypes contrasted in yield potential, a mega variety (IR64), a low-yielding variety reported as tolerant to high temperature (N22), and a high-yielding hybrid. Under increase in temperature from 28.2 to 35 °C tissue temperature, however, vegetative growth and seed yield of all the three varieties were reduced significantly, although the decrease with N22 was less than 50% of that of the two other genotypes confirming the tolerance to high temperature of that genotype. The positive effect of elevated [CO_2] reported on seed yield at 28.2°C was not measured anymore at 32.9 and 35.0°C (Madan et al, 2012).
In fact, the negative effect of temperature has even been widely reported to strongly overcome the positive effect of elevated [CO_2]. The prediction of climate change impacts on crop productivity has to address the combination of the adverse effects of elevated [CO_2] (positive) and temperature (negative) on plant functioning and growth processes. At 32.9°C, the high sink size of hybrid rice was enough to overcome some of the negative effect of temperature and set higher seed yield than that of IR64 (Madan et al, 2012). The diverse genotypic responses to temperature highlighted the challenge of assessing plant diversity response to combined elevated [CO_2] and temperature in order to improve genotypes in face of future climate scenarios. This challenge will get much gain from crop modeling if the relevant models are nicely calibrated with actual weather conditions, can provide accurate predictions of crop performance and appropriate ideotyping under future climate scenarios to guide crop improvement. Under the rice AgMIP network, the inter-comparison of the individual ability of 14 distinct rice crop models to simulate crop yield under future temperature and [CO_2] conditions highlights that the ensemble of crop models is well appropriate to conduct accurate predictions. Actually, one of the component I am quite involved is the gene-based crop modeling where the model parameters are expressed in function of relevant genetic markers so that models are able to simulate crop performance with respect to the genetic information. This will be of great help to molecular breeders as prediction tools of the crop performance of *in silico* genotypes.

The essential assessment of the combined effect of elevated [CO_2] and temperature and of the down-regulation of processes at elevated [CO_2] requires high-tech facilities where [CO_2] can be increased, and climate parameters can be precisely measured. Two types of facilities are relevant to host such studies. (i) Confined environments like growth chambers or compartments within greenhouses in which temperature and [CO_2] can be programmed with relatively high precision. In addition to monitor separately both factors in ranges that can simulate actual and future climate conditions, such facilities allow to conduct fine measurements in stable conditions, like steady-state gas exchange and non-soluble sugar concentration. Lacking in this kind of facilities at Cirad, I have invested a substantial amount of time pushing for its requirement and writing the scientific and technical document that served as a reference for the consolidated form finally submitted to the *Région Languedoc-Roussillon*.

Fortunately, the institute prioritized this demand into the list of investments submitted to the *Région*, and this was finally approved. Exploiting this newly dedicated experimental facility soon (to be inaugurated in 2017) at Cirad in Montpellier is really stimulating. (ii) Open fields equipped with a Free-Air CO_2 Enrichment (FACE) system: this is made of horizontal pipes forming a circle around the experimental plot, generally between 10 and 30 m in diameter, and emitting CO_2-enriched air to the internal plants. The FACE system provides the unique platform upon which to conduct genetic screening and elucidate the inheritance and mechanisms that underlie genotypic differences in productivity in real conditions under elevated [CO_2] (Ainsworth et al, 2008). Considering there is room for improving productivity and great challenges in investigating diversity within FACE, selection of promising genotypes and characterization of response mechanisms could then be effective since it is conducted close to the production environments. In this context, I was part of a team advocating for a new generation of large-scale, low-cost per unit area FACE experiments to identify the most CO_2-responsive genotypes and provide starting lines for future breeding programs (Ainsworth et al, 2008). Actually, the only FACE systems that have already been used and are available for growing rice, the Chinese and Japanese ones, are even not located within tropical areas, which reinforces the need of this type of facility in the tropical world devoted to annual crops including irrigated rice. One additional investment in the tropics would be the hosting within the FACE system of the T-FACE technology: this one is composed of rings of 4.5 m^2 equipped with six regularly distributed thermal radiators as infra-red heaters located at 2 m height (Peraudeau et al, 2015). Although the T-FACE technology is mainly reliable at night, the combination of both technologies would provide the appropriate facility to address some issues related to the combination of elevated temperature and [CO_2] in real conditions. Such investments are necessary if we are to realize the potential for yield gains in the future. Use one or the other facility, the confined or the FACE environment, has been a topic of controversy arguing, on one side, that the confined environment cannot be used to mimic the plant behavior in the real conditions and, on the other side, that the open field is characterized with high operational costs (CO_2 consumption) and questionable accuracy of the climate factors data. The best solution is certainly to combine both approaches.

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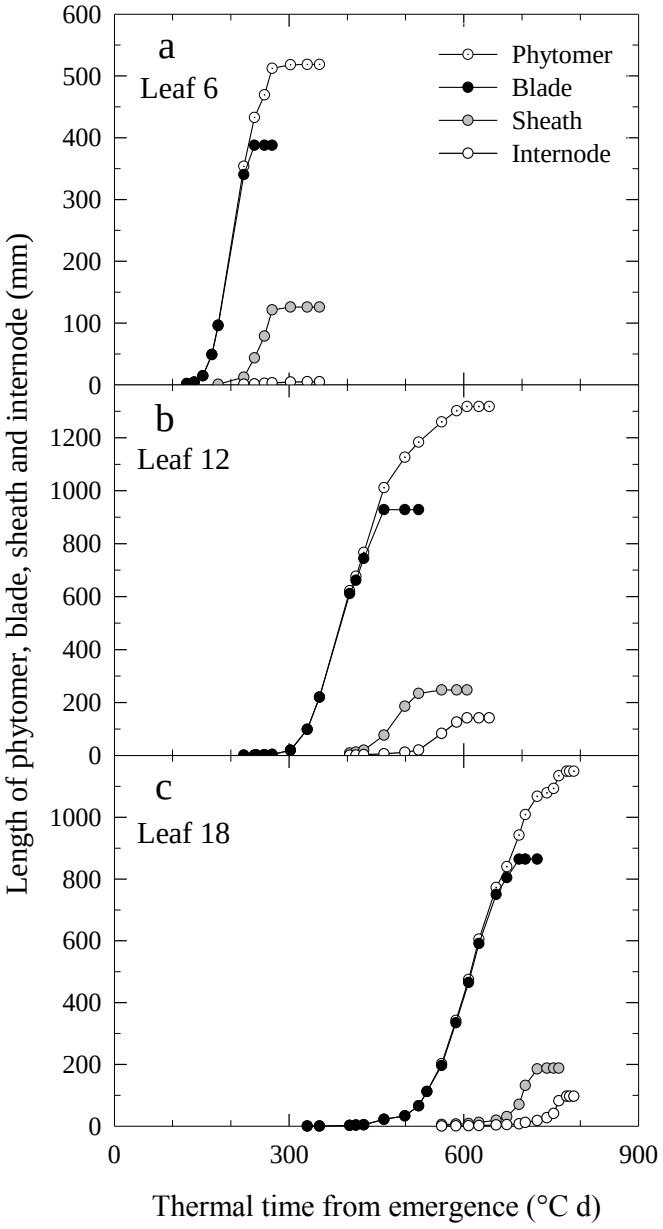

Figure 1. *Time-course of the elongation of blade, sheath, Internode and the whole phytomer of sorghum leaves 6, 12 and 18*

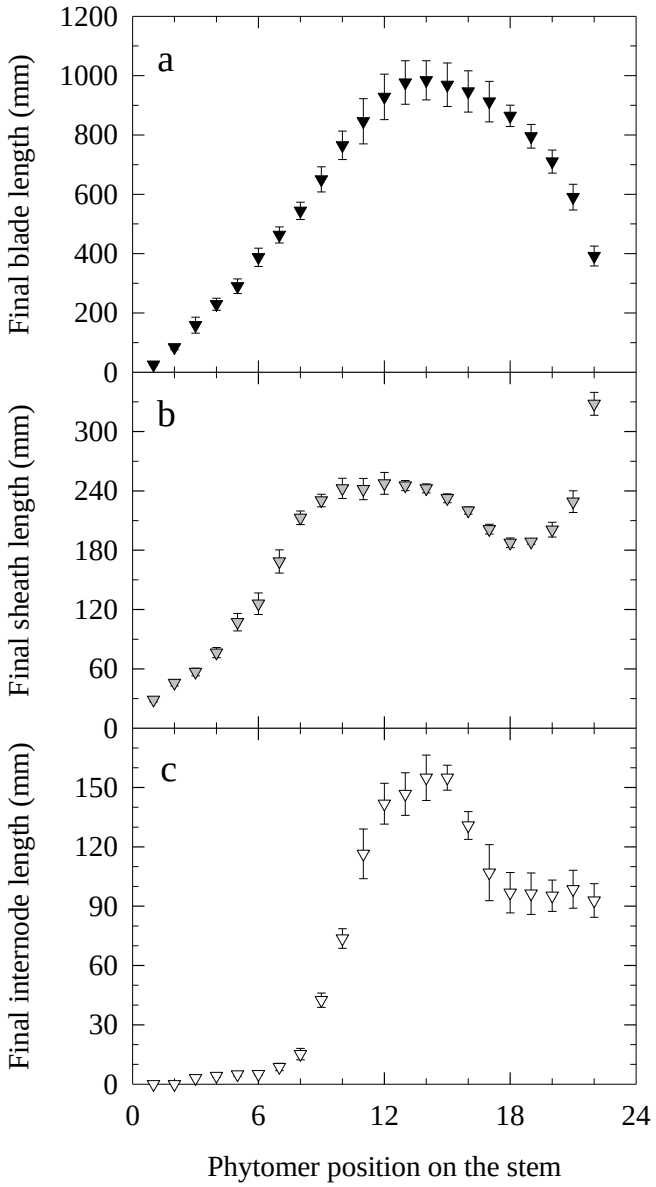

Figure 2. *Distribution pattern of the final length of sorghum blade, sheath and internode over phytomer position on the main stem*

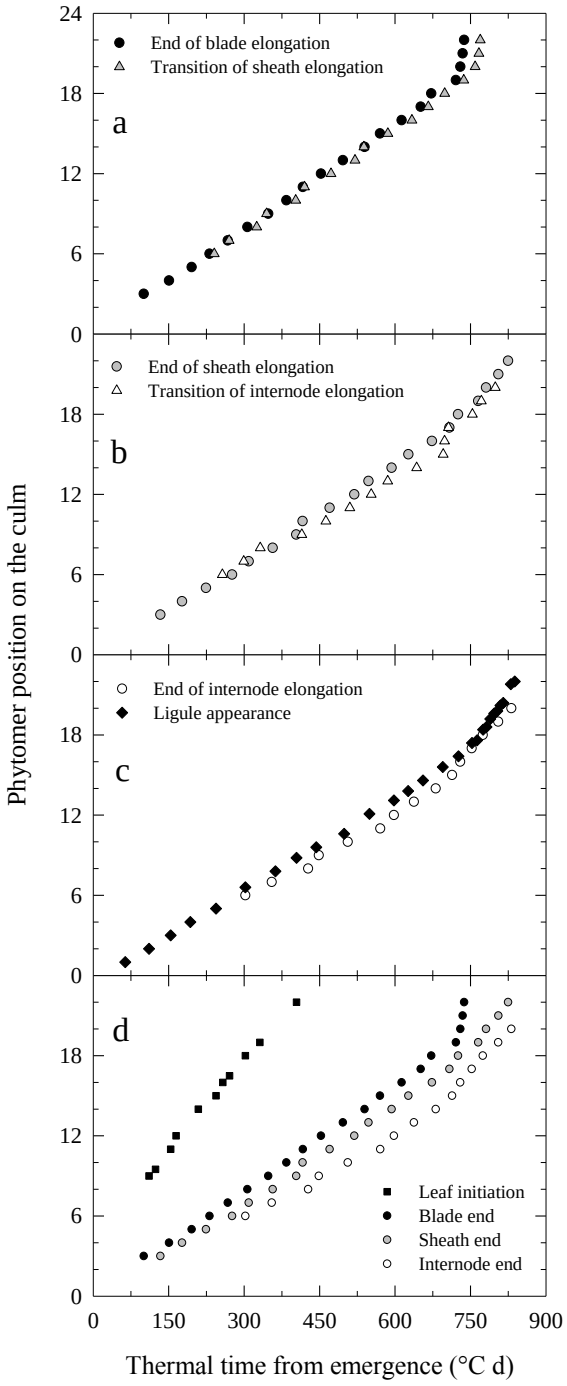

Figure 3. Position is sorghum of end of blade elongation, transition of sheath elongation phase between the cell division and cell elongation phase (as explained in Lafarge and Tardieu 2002), end of sheath elongation, transition of internode elongation, end of internode elongation, ligule appearance and a summary of leaf initiation, and end of blade, sheath and internode elongation with thermal time

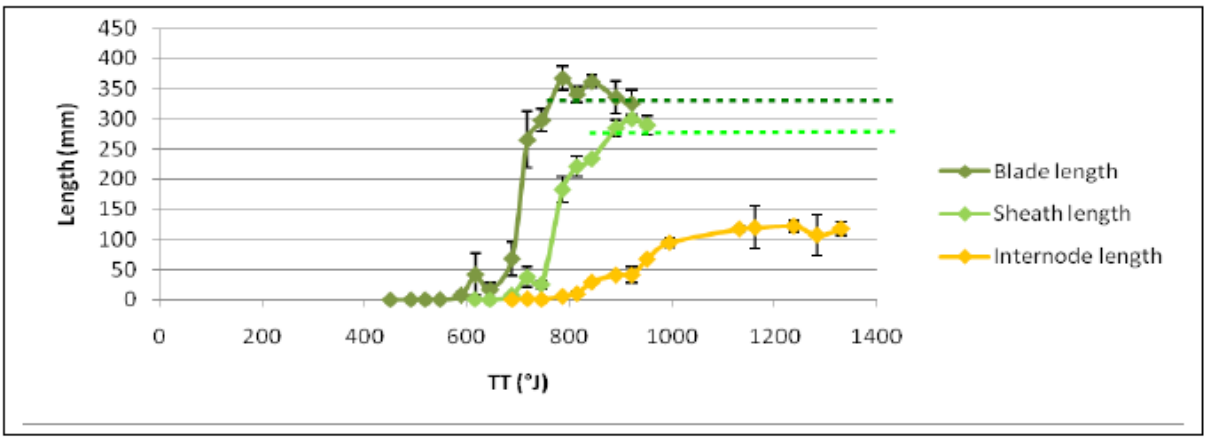

Figure 4. *Time-course of the elongation of blade, sheath, and internode of one rice upper phytomer*

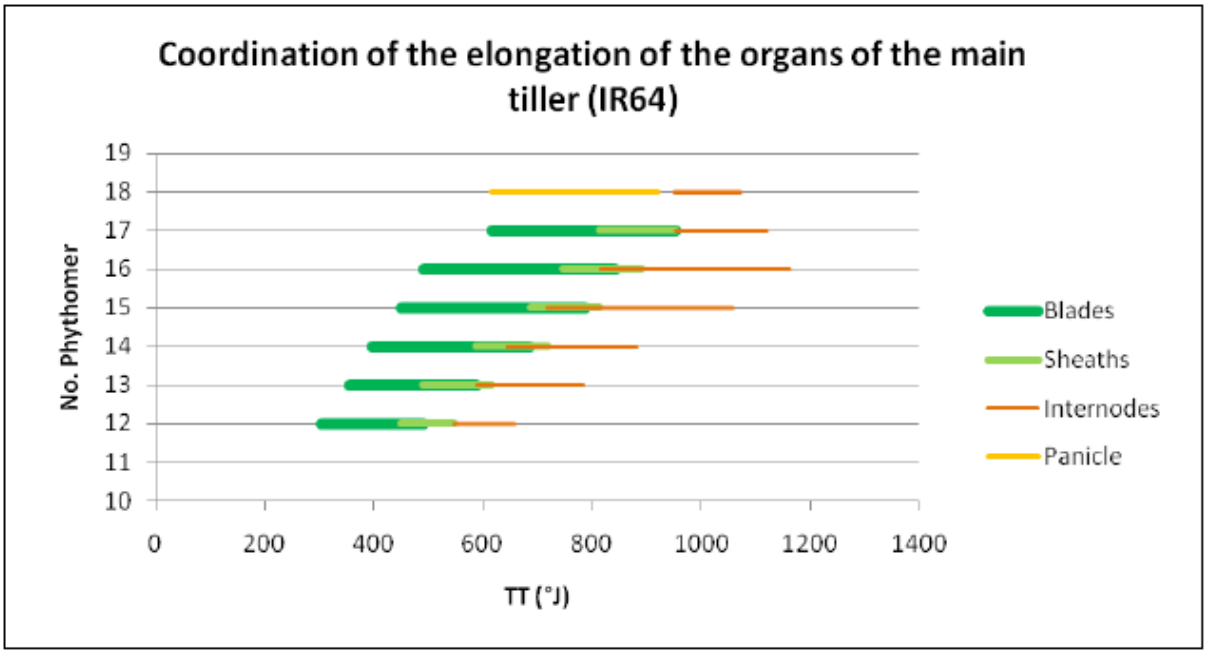

Figure 5. *Position in rice of the organ elongation phases of each phytomer with thermal time*

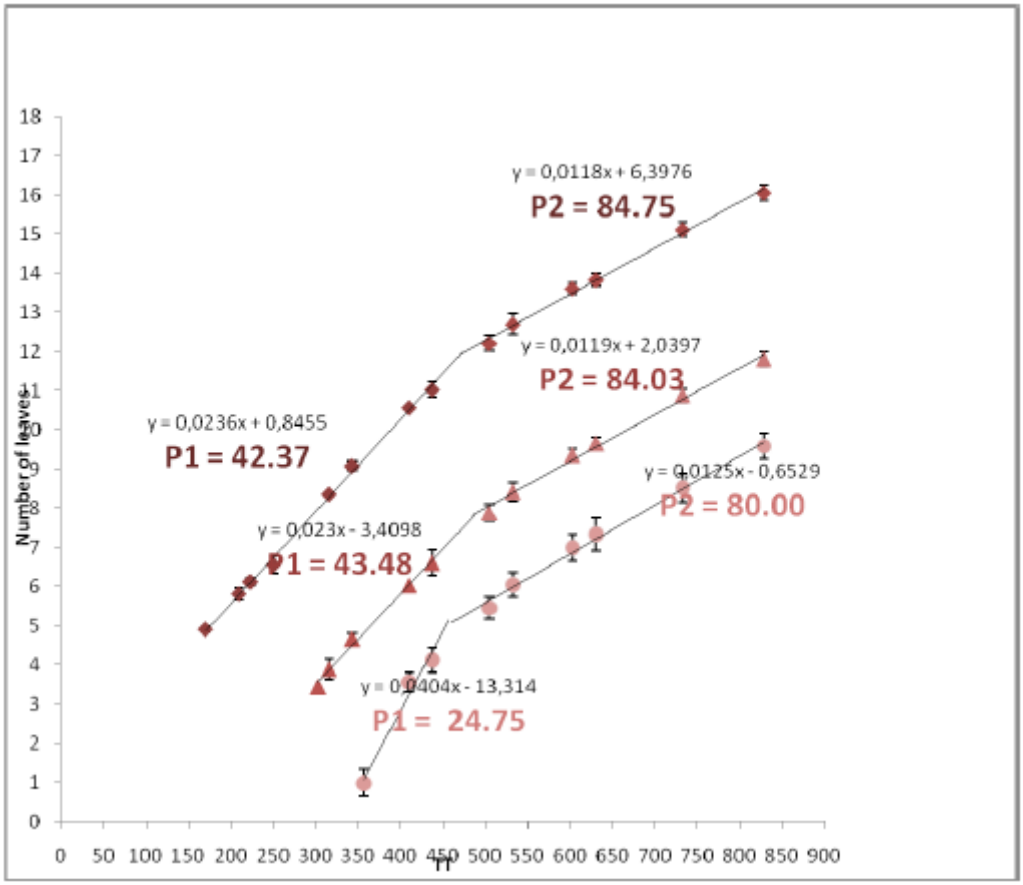

Figure 6. *Leaf emergence with thermal time of the main tiller (on top), a primary tiller (in the middle) and a secondary tiller (at the bottom) in rice*

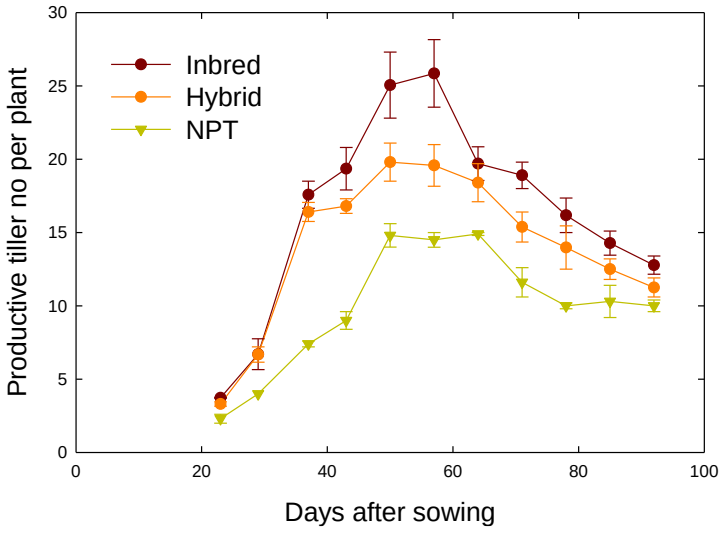

Figure 7. *Variation of tiller number in rice with time of an inbred variety, a hybrid rice and a NPT*

Graph 3.1

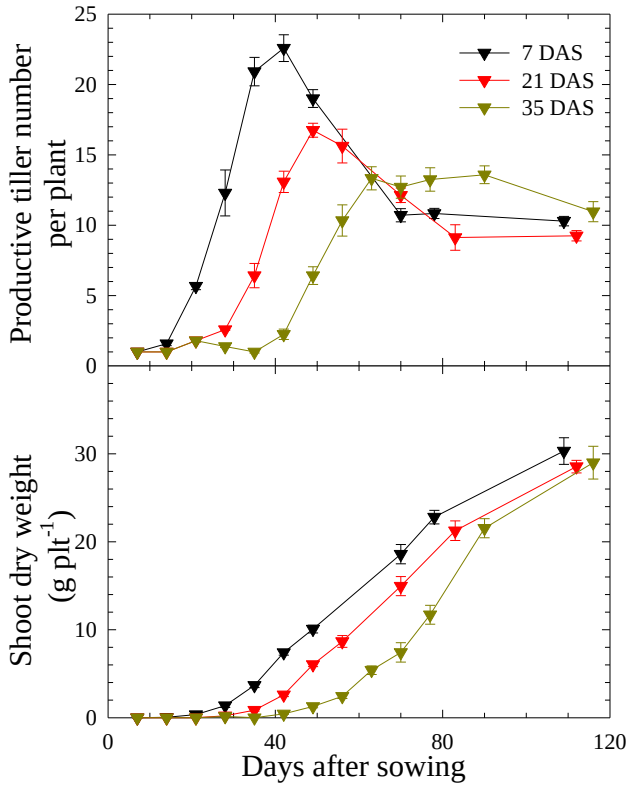

Figure 8. *Variation in time of the tiller number, and of the shoot dry weight, of the rice plant after transplanting the seedlings at 7, 21 or 35 days after sowing*

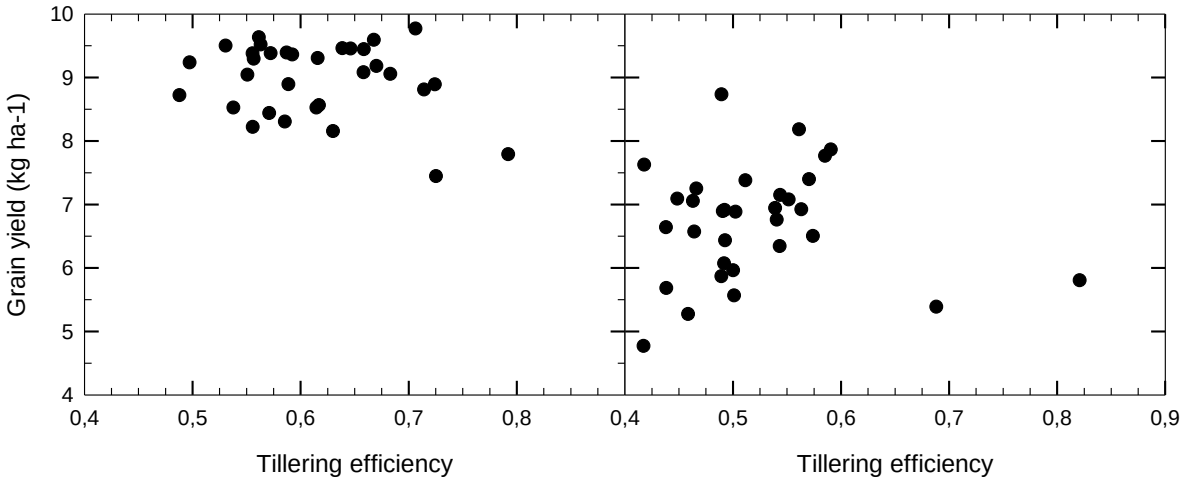

Figure 9. *Relationship between grain yield and tillering efficiency of 32 contrasted rice genotypes, during the dry season (graph on the left) and the wet season (graph on the right)*

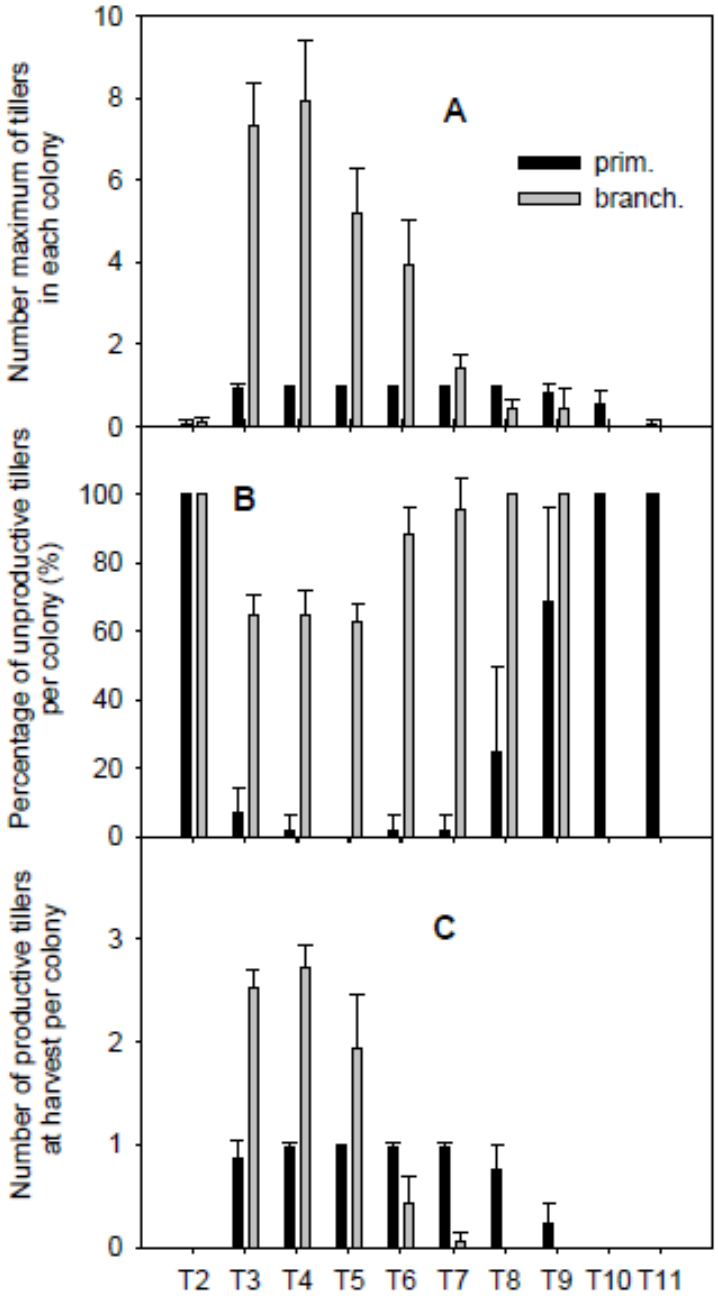

Figure 10. *Maximum number of tillers in each colony (graph on top), percentage of unproductive tillers per colony (graph in the middle), and number of productive tillers at harvest per colony (graph at the bottom) with respect to tiller origin in rice.*

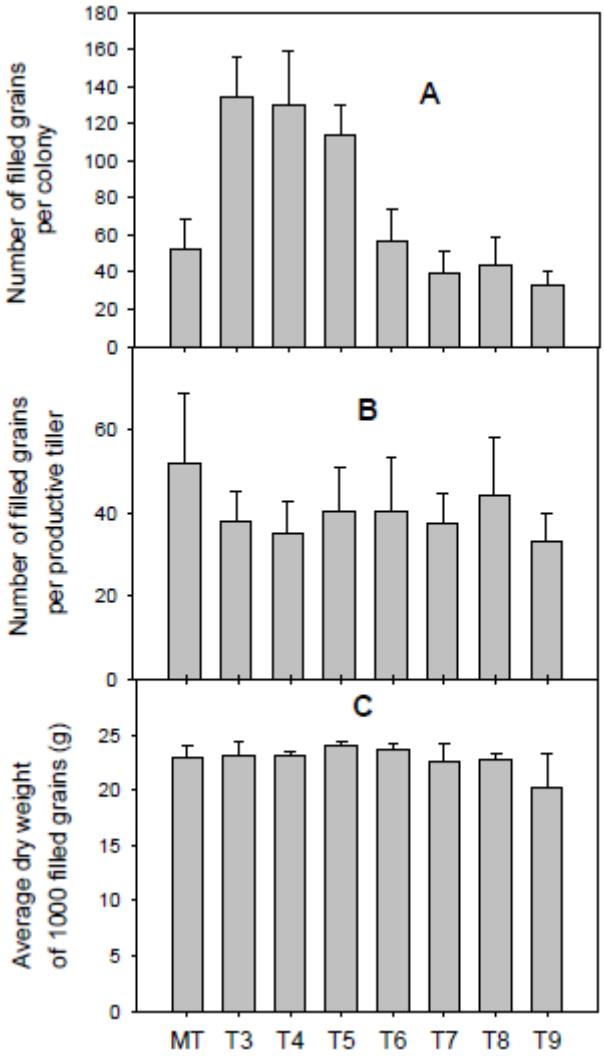

Figure 11. *Number of filled grains per colony (graph on top), of filled grains per productive tillers (graph in the middle), average dry weight of 1000 filled grains (graph at the bottom) with respect to tiller origin in rice.*

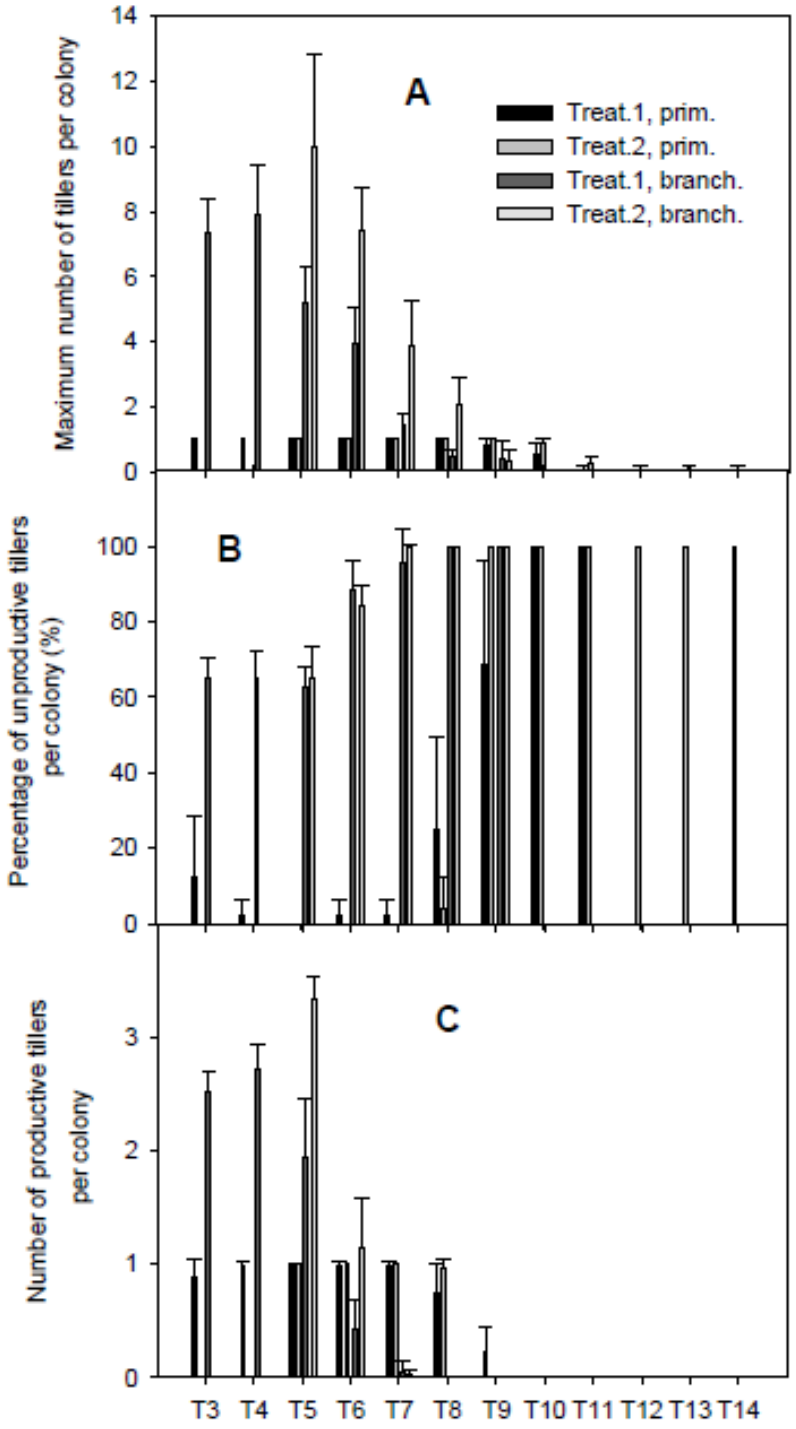

Figure 12. *Maximum number of tillers per colony (graph on top), percentage of unproductive tillers per colony (graph in the middle), number of productive tillers per colony (graph at the bottom) with respect to tiller origin in rice, considering treatment 1 as control plot, and treatment 2 as systematic removal of tillers 3 and 4, looking at the primary and the branch tillers.*

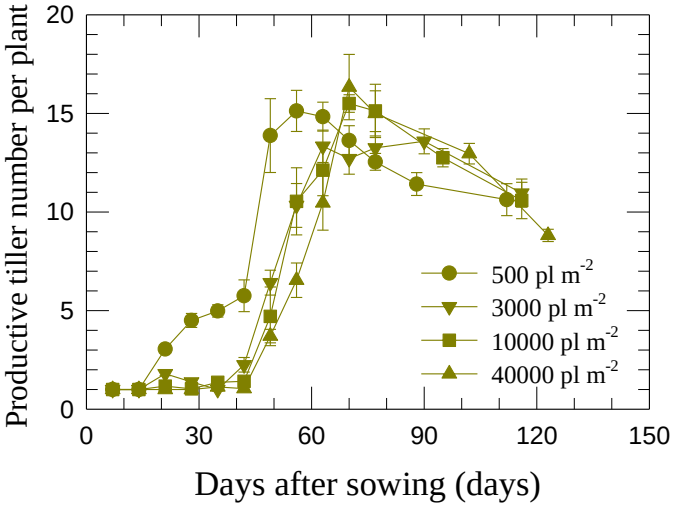

***Figure 13**. Change with time of the number of productive tillers per plant considering seed density in the nursery of 500, 3000, 10000, and 40000 pl m^{-2}. In this example, all seedlings were transplanted 35 days after sowing*

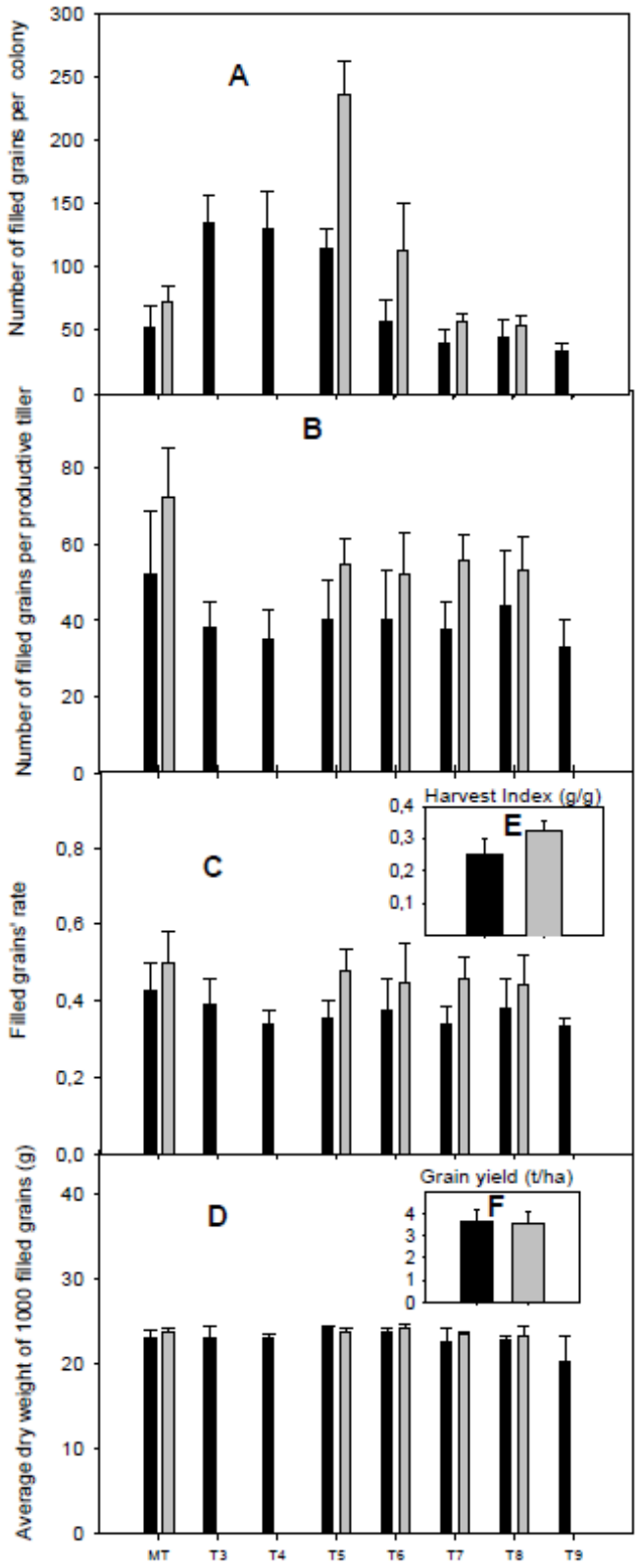

Figure 14. *Number of filled grains per colony, of filled grains per productive tillers, of the rate of filled grains, and average dry weight of 1000 filled grains, with respect to tiller origin in rice, considering the black bar as control plot, and the grey bar as systematic removal of tillers 3 and 4*

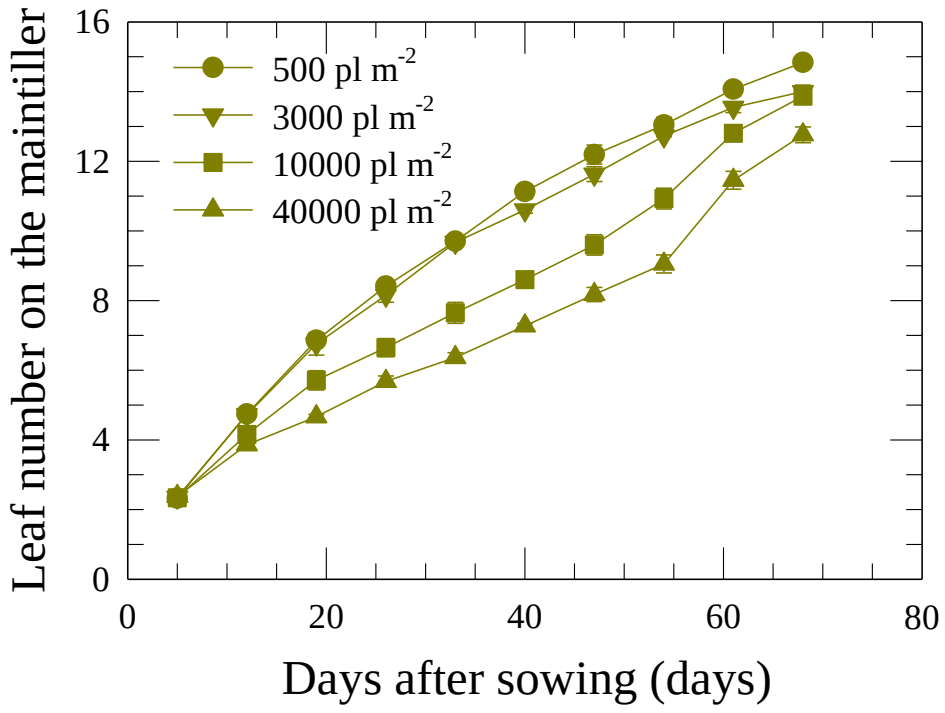

Figure 15. *Increase in leaf number on the main tiller with time for seed density In the nursery of 500, 3000, 10000 and 4000 pl m^{-2}. In all these cases, transplanting Was performed 35 days after sowing*

Research Project:
Improvement of the efficiency of grain filling and resources use under climate change constraints

A - Issues and challenges

Doubling crop production will be required by 2050 to provide the projected population at a satisfactory level, but in the context of reduction of arable land area and of detrimental impacts of future climate conditions. The most notable evolution among the climate changes is the increasing atmospheric [CO_2], which has risen from approximately 280 ppm in pre-industrial times to about 400 ppm nowadays, and will further increase to values of 470–570 ppm by 2050 depending on the climate scenario (IPCC Synthesis report, 2014). The resulting effect of elevated [CO_2] is higher leaf photosynthesis, and higher biomass and yield at crop level, although downregulation of photosynthesis at elevated [CO_2] leads to lower crop performance than that is expected. The positive effect of elevated [CO_2] is even accentuated with large sink capacity potentially fast-growing C3 species, like rice, that respond more strongly than slow-growing species (Horie et al, 2000; Liu et al, 2008). The relative magnitude of source and sink activities appears as an important determinant of crop yield under elevated [CO_2] (Lafarge et al, 2011). Although this increase in [CO_2] is expected to have a positive and significant effect on C3 crops production, it is counteracted by the rise in temperature (Parry et al, 2005) and in evaporative demand (Bolle, 2003). Global warming is one of the most challenging and burning issues for yield and quality crop production. Depending on the scenario for gas emission, an increase of 1.5-4.8 °C in average annual temperatures is predicted by the end of the century (IPPC Synthesis Report, 2014). Even though the COP21 agreement aims at limiting this rise at earth level at 2°C, consequences are already observed for both natural and agricultural systems with significant shifts in plant phenology, affecting in particular reproductive biology (Cleland et al, 2007). Environmental adverse conditions often cause early abortion and severe yield loss (2-16% every 1°C increase above optima (Battisti and Naylor, 2009)) and changes in chemical composition that may have dramatic implications for food safety (Ripoll et al, 2014; Halford et al, 2014). Clearly, climate change brings much uncertainty and complexity to this challenge for agriculture (Redden et al, 2011).

Improving nitrogen use efficiency through a reduction in N fertilization is an important requirement in the field in order to reduce N leaking in the soil and emission of N_2O in the atmosphere: even though N_2O concentration in the ozone layer has increased only from 0.27 to 0.33 ppm from the pre-industrial era to these days, it has a power of warming 298 times stronger than CO_2 explaining its toxicity (IPCC Synthesis report, 2014). Emission of N_2O are mostly due to human activities in the world of agriculture, like exploitation of swamps, utilization of N fertilizers, production of food for the livestock. In particular, soil fertilization corresponds to 11% of the emissions from the world of agriculture, the latter corresponding to 14% of the global emissions at the earth surface. Reducing N_2O emissions implies the reduction of N fertilization and the increase in nitrogen use efficiency (NUE) so that the plant can maintain its performance with less nitrogen uptake. As nitrogen is a key limiting factor for plant growth at elevated [CO_2] (Tuba et al, 2003), a better understanding of the processes involved in NUE in these conditions is expected. The increase in NUE is also expected to have a positive effect on the resistance to blast since the occurrence of this disease is well correlated with the N content within the plant through the Nitrogen Induced Susceptibility (NIS) index (Ballini et al, 2013). Here, the project will focus on subtending processes occurring during the grain filling phase which is relevant since NUE

is strongly dependent on processes on-going during that phase when N is remobilized from senescent tissues and possibly up taken at late stage from the soil.

One of the main target of breeding programs for higher yield potential in rice is a larger panicle. This is, in general, challenged at the whole plant level since taking into account compensation in-between yield components like panicle number, fertility and filling rate, and grain size is necessary: larger panicle size may be associated with fewer panicles per unit area, or with smaller grains, or with lower grain filling rate, and may not lead to higher yield in most cases. The main concept behind this objective is that higher sink strength per culm is the main driver of yield potential, or that high sink strength is strongly correlated with high C supply. Robust correlations between carbon availability and sink organ growth are, however, reported in the literature, which would indicate growth is mainly controlled by the source tissue. In my knowledge and from my experience, I tend to think that the elaboration of sink size during the reproductive phase is well aligned with potential C supply within the plant at the same time, while sink size and growth and sink regulation are the main drivers of source tissues during the grain filling phase.

Considering sink strength as the driver of grain filling is reinforced by the observation of the response of photosynthesis to elevated [CO_2]. Limitation of the positive effect of elevated [CO_2] on photosynthesis was reported: in practice, the average stimulation of C3 leaf photosynthesis under field conditions at elevated [CO_2] (550–600 ppm in Free Air CO_2 Enrichment, FACE) was only 14% on average across FACE experiments (Long et al, 2006)) where the expected increase was 38 % (Long et al, 2004)]. In rice, with a [CO_2] increase from 360 to 660-690 ppm, the increase in the photosynthetic rate was 30% to 70% at early stage, respective of the genotype, 30% at mid-tillering, but only 10% at maturity (Sakai et al, 2006), with an increase in crop biomass of only 15% to 30% at maturity (Lin et al, 1997). According to canopy-scale gas exchange measurements, this stage dependent response of photosynthesis to elevated [CO_2] was reported as the result of down regulation of photosynthesis (Sakai et al, 2006). In addition, at elevated [CO_2], the limiting sink strength of the plants seems to generate photo-assimilates accumulation in the leaf, reducing the triose-phosphate utilization (TPU) that is involved in Pi recycling TPU (Zhu et al, 2010), rubisco's activity and leaf N content, while increasing leaf C:N ratio (Hussain et al, 1999) and, at the whole plant level, accelerating leaf senescence (Paul et al, 2003). The carbohydrates accumulation, as a signal for down-regulation of photosynthesis, may be the evidence that field plants grown under CO_2 enrichment may not be fully adapted by lacking the adequate sink size (Ziska et al, 1996) and that rubisco is not limiting for photosynthesis under CO_2 enrichment.

Grain filling efficiency, not only depends on panicle size, but mostly on panicle architecture components like spikelet density (spikelet number over total branch length), branch number (distribution of branches respective of orders) and branch length. In fact, it appears more relevant to identify key component traits that may have a wider role than a given yield component. Alternative regulatory control mechanisms influencing C metabolism and/or plant growth under favorable conditions include sugar and hormonal signaling. There is growing evidence in several species that the trehalose-6-Phosphate (T6P) plays a central role in regulating carbohydrate and starch metabolism as well as the whole plant C source-sink relationships (Ge et al, 2008; O'Hara and Paul, 2013; Paul and Lawlor, 2014). Considering the diversified, eventually antagonistic roles of plant growth regulators in cell biology, it appears relevant to explore in details their influence on sink strength: ethylene negatively influences sink strength through interactions with starch synthesis and sucrose synthase

enzymes while auxin triggers apical dominance. Also, it is relevant to address how temperature and [CO_2] affect plant hormone activities and their influence on sink strength: higher panicle size obviously modifies the sink strength and the likely source:sink interactions which have to be analyzed under climate change scenarios and modified nitrogen fertilization.

1 - Sink strength and the regulation of the C source:sink interactions

The larger and more compact newly-bred panicle type is often associated with higher spikelet density within the panicle as breeders are focusing on larger spikelet number rather than on longer panicle length. Considering that the extension of the grain filling phase has not been associated with the selection for larger panicle, spikelet competition for resources is then expected to be stronger within a compact than a lax panicle as long as the phloem flux or the vessel section would not have increased proportionally to that of the panicle size. Traits related to vessel section, however, are not included in the breeding targets and might not have been co-selected with the large panicle trait.

Role of secondary metabolites in the regulation of sink strength through C and N metabolisms

The control of sink strength in crops selected for high grain yield may be under the control of the trehalose-6-phosphate (T6P), like the maintenance of sink strength of grain filling under abiotic stress in maize (Nuccio et al, 2015). Indeed during the course of development of wheat grains, amounts of T6P was excessively high in the whole grain and decreased with time until maturity, and this pattern was correlated with that of sugars although the dynamic range of the latter was lower (Martinez-Barajas et al, 2011). In fact, the mechanistic basis for the signaling function of T6P in growing tissues involves the inhibition of the sucrose-non-fermenting-1-related protein kinase (SnRK1) in response to sugars availability (Zhang et al, 2009): as antagonistic, T6P inhibits SnRK1 activity when sucrose level is high, and SnRK1 activity is high, and T6P levels reduced, when sucrose level is low. In response to sucrose, T6P regulates gene expression for growth and development through the protein kinase SnRK1. T6P was also confirmed as a potentially significant component of the regulation of SnRK1 in wheat grain: changes observed in T6P levels during grain filling were associated with changes in SnRK1 gene expression, with inhibition of SnRK1 up to 10 days after anthesis and activity of SnRK1 beyond this stage (Martinez-Barajas et al, 2011). There was, however, tissue-specific patterns: before 10 days after anthesis, T6P levels were high, and SnRK1 activities low, in all tissues of the grain. Beyond 10 days after anthesis, even though sucrose content was high in all tissues, high T6P levels were confined to the endosperm, where it activates starch synthesis; SnRK1 activity was not inhibited by T6P in the embryo and pericarp where it was involved in the development of the embryo.

Trehalose-6-phosphate (T6P), as the metabolic precursor of the non-reducing disaccharide trehalose, is an essential signal metabolite in plants (Paul et al, 2008). It is synthetized from glucose-6-phosphate and UDP-glucose by trehalose-6-phosphate synthase (TPS), and metabolized to trehalose by trehalose-6-phosphate phosphatase (TPP) (Cahib and Lenoir, 1958). The T6P appears as a central metabolite to several growth and developmental processes since the consequences of activities of TPS and TPP were reported as opposite in Arabidopsis thaliana: overexpression of TPS generated early-flowering, small leaves and highly branched inflorescence while overexpression of TPP resulted in late-flowering, large leaves and less branched inflorescences (Schluepmann et al, 2003). Clearly, the amount of T6P is

determined by the relative rates of synthesis by TPS and dephosphorylation by TPP, and plants with reduced T6P content could not make efficient use of supplied sugars and experienced growth inhibition. Yadav et al (2014), who analyzed the response of C-starved *A. thaliana* seedlings after feeding with either, sucrose, glucose or fructose, observed that T6P was highly correlated with sucrose, more than with glucose of fructose. This suggested that T6P levels serve as a signal for high carbon availability in the form of sucrose, and that sucrose content had a direct impact on T6P levels. By growing lines of *A. thaliana* overexpressing constitutively either TPs or TPP, Yadav et al (2014) confirmed the role of T6P as signal metabolite for sucrose status in plants, where correlations with other nutrients are indirect and mediated via sucrose levels. They have proposed that the ratio T6P:sucrose is a critical parameter for the maintenance of sucrose levels within an appropriate range. It has been proved in maize that harvest index and grain yield under well-watered or water deficit conditions can be increased by changing sucrose metabolism through overexpression of TPP, and so reduction of T6P levels, during grain filling (Nuccio et al, 2015). It is suggested that the decrease of the T6P:sucrose ratio may have induced higher sucrose available to the spikelets through increase in SnRK1 activity. The approach of modifying T6P in specific sink tissues provides a novel and rational means of increasing crop performance.

Leaf senescence, as a key process occurring during grain filling and essential source of N remobilization, is not a passive and unregulated process. It is influenced by various internal and environmental cues, including light intensity, temperature and drought. Also, plant hormones play an important role in the regulation of leaf senescence. Indeed, strigolactones appear to regulate leaf senescence. Ueda and Kusaba (2015) reported that leaf senescence is accelerated by the application of strigolactones in the presence of ethylene and not by strigolactones alone. They suggest that strigolactones promotes leaf senescence by enhancing the action of ethylene. The combined role of ethylene and strigolactones on the regulation of leaf senescence suggest to consider both hormones together while analyzing the physiological processes involved during the dynamics of grain filling

Sink strength, panicle architecture, starch accumulation and role of ethylene

Filling of individual spikelets is widely reported as position dependent, with apical spikelets filling earlier and maturing earlier than basal spikelets (Ishimaru et al, 2005). Indeed, endosperm is the storage tissue of assimilates (sucrose), and endosperm cell number, which increases during the post-anthesis period, is higher in the apical spikelets, and so is the endosperm volume, due to the difference in cell division rate (Kuanar et al, 2010). Assimilates are transported from the phloem terminal of the seed coat to the maternal tissue (pericarp) during the early part of endosperm development, released in the free space of the embryonic apoplast before being stored in the endosperm, which determine the final seed weight. Sink activity for the utilization of sugars by the endosperm is then correlated with the cell number of the endosperm and the concentration of these solutes in the apoplasmic space which varies positively with the size of spikelets and with grain growth, and is lower within basal spikelets (Kuanar et al, 2010). In addition, the total protein and chlorophyll concentration of the pericarp and endosperm of the apical caryopses contain higher concentration of materials than that of the basal caryopses. The endosperm of apical spikelets gets higher priority in partitioning of assimilate with higher subsequent concentration of starch, whose biosynthesis pathway is controlled by the activities of enzymes including sucrose synthase (SS) and ADP glucose pyrophosphorylase (AGP). Activity of SS is a potential indicator of the early rate of grain filling, while activity of AGP would be a good indicator two weeks after anthesis. With time, the concentration of soluble sugars is lower, and

the accumulation of starch higher, in the apical spikelets as activity of SS and AGP is higher (Mohapatra et al, 2009). Growth of apical spikelets is then quicker and longer.

High ethylene production in the basal spikelets retarded pericarp development and was negatively correlated with starch synthesis enzymes and rates of cell division and grain filling of the endosperm (Panda et al, 2009). Ethylene production, which is known to increase in the pre-anthesis period and peak at time of anthesis and decline thereafter, is also reduced in the apical spikelets and large seeds compared to the basal spikelets (Wang et al, 2012). Significant and positive correlations were observed between ethylene concentration and peroxidase activity, which was higher in the basal caryopses (Kuanar et al, 2010). As a result, excess of CH solutes in the basal spikelets stays as soluble sucrose in the endosperm, is not converted to starch, and so does not fill the spikelets (Sekhar et al, 2015). In addition, it has been reported that a low content ratio of ABA to ethylene would retard grain filling. Clearly, ethylene concentration influences sink strength of the growing endosperm. In fact, cell number and activities of SS and AGP determine sink strength, and that would be down-regulated by ethylene production (Mohapatra et al, 2009) which would offset the balance between ABA and ethylene.

This strong apical dominance of the grain located on the apical branches results in significant variation of single rice grains within a panicle. This issue shall even become more important within the large and compact panicles of the newly developed rice cultivars. Action of ethylene has indeed been measured more intense in high density panicles (Panda et al, 2009). The hypothesis here is that sink strength of the whole panicle could be increased over time if apical dominance within the panicle would be reduced, and so if more spikelets would be filled at the same time. This pattern of grain filling is then expected to be associated with larger peduncle section to meet with the likely higher CH flux within the phloem. Interestingly, some recent results obtained in the project *DRYCE* that I coordinate indicates that there is a strong correlation between the number of spikelets of the panicle and the diameter of its upper internode, the one just below the peduncle.

Few options could be evaluated to reduce apical dominance. (i) Effects of overexpression of TPS in transgenic tobacco plants generating abnormally high T6P contents induced a loss of apical dominance (Romero et al, 1997; Goddijn et al, 1997) and an increase in photosynthetic activity (Pellny et al, 2004). This indicates that T6P is one of the metabolites involved in the apical dominance and that manipulating rice plants by feeding them with solutions of T6P would be one way to evaluate the reduction of apical dominance on sink strength. Other options related to the regulation of sink strength by C metabolism, hormones, sugar signaling and hydraulic processes need to be evaluated by large-scale comparisons between contrasted genotypes for sink strength. (ii) Sink strength of the whole panicle could be increased if ethylene production would be minimized within the basal spikelets for the sake of fast-synchronized filling. On one hand, the G x E interactions on ethylene activity during grain filling and the level of heritability of this process would be determined through targeted trials and whether some growing conditions would minimize ethylene activity would be identified. On the other hand, ethylene impact could be lower by growing plants with laxer panicles. This can take different directions: (a) increased spikelet distance within the panicle by increasing primary branches number, without increasing spikelet number and panicle length, (b) increased panicle length without increasing spikelet number, and (c) increased panicle number with smaller panicles.

2 - Sink strength and the uptake and remobilization of nitrogen

Nitrogen uptake is stimulated by the increase in crop growth rate of the plant, i.e. the increase in sink strength (Lemaire et Salette, 1984), but this is counterbalanced by the increase in amino acids and nitrogen content by unit of leaf area (Gastal et Lemaire, 2002 ; Miller et al, 2008). Stimulation of nitrogen uptake by photosynthesis confirms its regulation by the carbon status of the plant (Lillo, 2008). And the positive regulation of nitrate transporters is correlated with the rate in glucose 6-phosphate (Wirth et al, 2007). A transcriptomic study reported a strong role of nitrate in the regulation of the genetic control of nitrogen uptake, coordinating carbon and nitrogen metabolism (Scheible et al, 2004). In contrast, root morphology has limited effect on nitrogen capacity from the soil due to the high mobility of nitrate, NO_3^-, and ammonium, NH_4^+ (Robinson and Rorison, 1983).

Nitrogen assimilation takes place in both root and shoot tissues. Nitrate is reduced into nitrite (nitrate reductase activity), then into ammonium (nitrite reductase activity). Ammonium is assimilated into amino acids, then integrated into the proteins that contain the majority of plant nitrogen (Sage et al, 1987). Within cereals, during the post-floral senescence, nitrogen is remobilized, released into the phloem as amino acids, mainly glutamine, and transported up to the panicle where it is integrated into grain proteins (Masclaux-Daubresse, 2010). In wheat, nitrogen remobilization concerns up to 60 to 95% of grain nitrogen at maturity (Martre et al, 2003 ; Barbottin et al, 2005 ; Kichey et al, 2007) and is nicely estimated by the nitrogen harvest index (NHI), i.e. grain nitrogen divided by shoot nitrogen (Masclaux-Daubresse, 2010). Rapid leaf senescence is often associated with strong nitrogen remobilization (Uauy et al, 2006) while delayed senescence, reported as the *stay-green* trait, is beneficial to crop photosynthetic activity (Foulkes et al, 2009a). Indeed in wheat, nitrogen uptake after flowering, from 5 to 40% of grain nitrogen, is correlated with nitrate reductase activity, while nitrogen remobilization is correlated with glutamine synthetase activity (Kichey et al, 2007).

The predominant part of remobilized nitrogen into grains at maturity, so up taken before flowering (Hirel et al, 2007), suggests that (i) remobilization as nitrogen source for grain filling is a substitute for post-floral uptake and (ii) senescence, and so reduction in carbon assimilation, is an early process that takes part soon after flowering. This reduction detrimental to carbon assimilation could be limited, and stay-green favored, if post-floral uptake would be stronger. Post-floral uptake and rapid nitrogen transfer to the grains could be associated with starch remobilization from internodes (Foulkes et al, 2009b). Early or delayed senescence was reported in *A. thaliana* when SnRK1 genes were either silenced or overexpressed, respectively (Baena-Gonzalez et al, 2007): this suggests that the interaction between T6P and SnRK1 is important for signaling sugar availability to regulate leaf senescence (O'Hara et al, 2013). The involvement of T6P in the regulation of leaf senescence in response to sugar availability may play an important role in the nitrogen post-floral uptake and its transfer to the sinks (Wingler et al, 2012). Strigolactones are also key metabolites involved in the regulation of senescence (Al Babili and Bouwmeester, 2015). The increase in nitrogen uptake after flowering may also have a major effect on nitrogen use efficiency (NUE) in better exploiting the soil nitrogen resources. This should have strong environmental, economics and societal beneficial impacts (Xu et al, 2012 ; Garnett et al, 2013) considering that cereal improvement during the last decades was preferentially conducted under conditions of high nitrogen availability (Cormier et al, 2013; Garnett et al, 2015).

The simplest calculation of NUE is the production of biomass or grain per nitrogen unit utilized (Good et al, 2004). By extension, the nitrogen agronomic efficiency (the difference in grain yields divided by the difference in nitrogen fertilization) provides a tool to compare genotypes in their ability to value an extra fertilization of nitrogen relative to a reference amount (Dobermann, 2005). Substantially, NUE

can be decomposed into uptake and utilization efficiency, which measure the ability of the plant to extract nitrogen from soil, and to convert soil nitrogen into grain nitrogen, respectively. Relative to flowering time, the uptake efficiency can be break down into pre- and post-floral components, and the utilization efficiency into pre-floral nitrogen remobilization and post-floral nitrogen transfer (Kichey et al, 2007). Considering that the remobilization efficiency is correlated to nitrogen pre-floral uptake, and that 90-95% of post-floral nitrogen uptake is transferred to the grains, as observed in wheat (Kichey et al, 2007), the remobilization efficiency and post-floral uptake efficiency appear as the key components of NUE and of the characterization of phenotypic diversity. Because of the involvement of N and C source:sinks relations into the determination of NUE components, some phenotypic markers of crop performance with respect to NUE may involve some sink strength components.

B - Objectives and methodologies

The focus on post-flowering processes appears as of great agronomic and breeding interest as it involves various adaptive and innovative strategies, which include C and N assimilation and reserves mobilization, metabolite signaling, panicle architecture patterns, stem anatomy, leaf senescence dynamics, with the goals of higher grain yield, better adaptation to climate change, higher nitrogen use efficiency, and possibly higher resistance to blast.

1. Objectives and scientific questions

The main objectives of this project are to (i) identify the morphological patterns and physiological processes during the grain filling phase driving higher yield and (ii) reveal QTLs and candidate genes governing the relevant traits. The main hypotheses of this project are that (a) sink strength is the main driver of grain yield during this phase and (b) sink regulation is the main component acting on sink strength, considering that sink size (panicle size x panicle number) meets expectations. This last claim is supported by the systematic appreciable ratio of unfilled spikelets measured at maturity under favorable growing conditions. One component of sink size, however, the phloem section within the peduncle, may not be aligned with the instantaneous potential demand of the large panicle, and will need to be considered carefully within this study. Sink regulation will be analyzed in terms of the dynamics of grain filling along the panicle in relation with panicle architecture and molecular signaling directly involved in sugar (ethylene, T6P) and nitrogen (strigolactone, glutamine) dynamics. In particular, the direct effect of sink regulation on the balance between remobilization and assimilation of C and N, on the distribution of C and N at the whole plant level, and on the plant nitrogen use efficiency, will be studied. The main hypotheses described here imply that sink strength is controlled by whole plant signaling in relation to local plant C status but independently of whole plant C status (plants are sink limited). It appears that the adaptive response of seed filling is the consequence of multiple inter-connected processes and molecular signals. Elevated [CO_2] and higher temperature will modify these regulatory mechanisms and how these modifications will affect sink regulation will be taken into account here.

The subtending questions relevant to this project are as follow:

- At similar spikelet number, is sink strength higher with many small or few large panicles?

- Are high-sink strength varieties favoring rapid leaf senescence and N remobilization or delayed leaf senescence and high crop photosynthesis during grain filling?
- Are high-sink strength varieties stimulating leaf photosynthesis through quicker and higher export of non-soluble carbohydrates from the source leaves to the sink tissues in the panicle?
- Is dominant effect between spikelets along the panicle more pronounced, and is grain filling ratio higher, in compact (more secondary and tertiary branches) or lax (longer with more primary branches) panicles?
- Is nitrogen use efficiency correlated with post-flowering soil uptake and/or sink strength or panicle size?
- How are these processes modified at elevated [CO_2] and higher temperature?

Some candidate genes or larger QTLs have already been revealed for some of the above-mentioned traits like some related to panicle size, T6P, and starch and soluble sugar and glutamine biosynthesis pathways. Through mutants or introgression lines, this will allow the dissection of the targeted physiological processes, the detection of candidate genes if necessary, and the quantification of genetic expression of these genes involved in panicle architecture, and sugar and nitrogen dynamics within the plant. In addition, diversity panels and small sub-populations (50-100 genotypes) composed of a target genetic diversity for a relevant trait could be evaluated to reveal new QTLs/genes or confirm candidate genes, and to better quantify the range of variation of candidate traits. Also, whole plant physiological processes shall be dissected and analyzed within sub-groups (10-15 genotypes) formed of contrasted breeding programs lines and relevant genetic materials to identify phenotypic markers, either phenological, morphological or biochemical, that account for the crop performance.

These studies will be mainly conducted within distinct field locations to have access to contrasted climate conditions and under well targeted timing and amount of N fertilization. As a complementary and essential study, these sets of genotypes will be also grown under controlled conditions with well targeted conditions of temperature and CO2, exploiting the new facilities of greenhouse compartments and growth chambers set up at Cirad.

2. Approach and methodology

This project will value the phenotypic diversity that is already available on panicle size and architecture within some main breeding programs, as larger and more compact panicles are the focus of many of them. This is the case of those I am in interaction with, the conventional breeding program conducted at IRRI (Philippines), IPB (Indonesia), and Embrapa (Brazil), and the hybrid rice breeding program at IRRI (Philippines) and CIAT (Colombia), and the team of Pf Mohapatra (Sambalpur University, India). In particular, one breeder from IPB has progenies contrasted in panicle size with up to 350 spikelets per panicle, either within compact or lax panicles, and some contrasted in dominance effect for grain filling. Some NILS from a mapping population for panicle size with the IR64 background are shared between IRRI and Japan with variability in branch number and length. These NILs are those that I have studied in details during the PhD thesis of Dewi Erika Adriani and where the identified QTL for large panicle has in fact an earlier effect on tillering dynamics. In addition to contrasted fixed progenies from breeding programs, some diversity panels are particularly of relevance, like the Vietnamese and African panels shared by IRD and the local organization, which provide a large diversity for the component traits of the panicles. Some interesting mutants, if any, could be included as well.

Including some diversity for NUE within the population of indica genotypes considered in this study will be an added value. Genetic diversity for NUE has been characterized within the tropical japonica sub-specie in a project, *GS-Ruse*, initiated in 2013 within the joint Cirad-Fofifa breeding program conducted in Madagascar. Which traits to consider to capture NUE diversity is still under question. However, the project in Madagascar resulted in the development of protocols to evaluate NUE in the field, and in functions to calibrate NIRS (near-infrared spectrum) values to the quantification of leaf and grain N content. This open avenues to a straight-forward characterization of NUE in a new panel. In addition, a trait such as the dynamics of leaf senescence shall also be a strong candidate. These traits will soon be evaluated in a new project in which I am involved, *SEPYA* (with UMR BGPI as a partner), that will start in 2017 and will aim at characterizing NUE and the nitrogen induced susceptibility to blast (NIS) on a panel of temperate japonica in Camargue, South of France. The challenges will be to detect if a diversity exists in the post-flowering N uptake, if this process is related to delayed leaf senescence and higher NUE, and if higher NUE and lower NIS are correlated. Our partner, UMR BGPI, has already some interesting candidate genes to focus on.

The main traits governing panicle size and nitrogen dynamics will be confronted to genetic studies to investigate whether they are governed by many genes, and with or without high heritability. Some molecular markers could be, first, identified for some metabolites for which candidate genes are not known. This could use metabolomics data for genome wide association studies (GWAS) with a high level of detection (soluble sugar concentration, starch synthesis enzymes, glutamine, strigolactone). Non-structural carbohydrates (NSC) have already been confirmed as a relevant biological scale to tackle genotypic diversity in terms of shoot growth. Candidate genes involved in the activities of some key metabolites described here (T6P, …) are already known from studies on *Arabidopsis Thaliana* or others (….), so some detection for polymorphism of allelic diversity of these genes could be conducted on a diversity panel so that a sub-population of balanced polymorphism could be constituted, but with genotypes with similar plant height and crop duration. Some small panels (10-15 genotypes) could be constituted for the functional validation of these genes (allelic effect in response to contrasted N fertilization for example).

One of the main challenges in modelling is to improve the biological significance of current ecophysiological models by refining the description of biological processes and better integrating available “omics” information. Both Ecomeristem and Samara models, the two crop models developed by our team, have the originality to simulate daily plant/crop nutritional status as ratio between water or carbohydrates supply and demand. These state variables are used to regulate either sink or source functioning and thus crop growth and performance respective of environment and genotype (response parameters). It is a requirement now to improve them by including some N dynamics. Widely, nitrogen concentration in the plant is taken into account in models via the nitrogen dilution curve that gives a good evaluation of nitrogen content in the plant but does not allow the characterization of genetic diversity and the G x E. Considering both models are targeting the characterization of phenotypic diversity for different processes, the nitrogen dilution curve approach does not seem appropriate. The improvement of both models with a process-based nitrogen module may be the way forward, but at the same time, environmental effects and G x E interactions have to be considered as well by the models. The product developed by Bertheloot et al (2008) should be a strong starting point from which to develop this work. Because the Ecomeristem model relies on a detailed and dynamic representation of plant morphogenesis at organ level, controlled by genotypic potential parameters), it appears more

adapted to integrate parameters describing the diversity of panicle architecture. This is also an issue that interests the team of Hiroe Yoshida (NARO, Japan). Much needs to be done to address this issue.

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Résumé des recherches et du projet en français

La majorité de mes recherches s'inscrit dans le contexte des interactions source:puits, et plus particulièrement de la mise en place des puits et de leur régulation, et a pour objectif principal la détermination de marqueurs phénotypiques pour l'amélioration des rendements du riz irrigué. L'analyse des résultats se concentre d'abord sur la dynamique de mise en place des structures aériennes du peuplement, avec un accent sur les dynamiques et plasticité du tallage et de la surface foliaire spécifique, selon un axe de comparaison sorgho-riz. Nous les avons principalement étudiées en réponse d'accès à la lumière (ombrage, densité de peuplement) en nous concentrant, pour le riz, sur le différentiel entre riz hybrides et variétés améliorées. La meilleure régulation des puits observée chez les hybrides et chez une NIL, introgressée avec un QTL d'augmentation de la taille de la panicule, a été une explication majeure de performances plus élevées. La comparaison entre riz et sorgho montre, qu'au-delà de fortes similitudes, une différence essentielle est celle relevant de la mortalité des talles, qui ne semble pas affecter le rendement du riz, à la différence du sorgho. Même si elle est bien tamponnée, la plasticité de la surface foliaire spécifique apparaît comme la première variable d'ajustement de la plante, notamment pour le maintien de la dynamique de tallage. Ces résultats sont notamment discutés dans un contexte de modélisation. L'adaptation face aux évolutions du climat, ici l'augmentation de la température nocturne et diurne, a été prise en compte dans mon travail sur deux processus bien définis, la respiration et la fertilité des grains. Nous avons confirmé que la respiration augmente avec la température nocturne, mais que cette augmentation n'a pas d'incidence significative sur la biomasse et le rendement. En revanche, nous avons identifié que la relation communément employée dans les modèles d'un doublement de la respiration pour une augmentation de la température de 10 °C (Q10 = 2) était erronée et plus proche, en conditions d'acclimatation, de la relation Q10 = 1.5. Par ailleurs, une liste de 14 SNPs de loci indépendants impliqués dans la tolérance de la fertilité à la chaleur a été identifiée par phénotypage d'un panel de diversité, dont plusieurs colocalisent avec des QTLs connus pour leur implication dans la tolérance à la température élevée.

Le projet que je propose pour les prochaines années s'appuie sur le résultat principal de mes travaux antérieurs : l'importance de la régulation des puits dans l'élaboration du rendement. Après avoir ciblé la phase d'élaboration de la structure foliaire de la plante, je souhaite dorénavant concentrer mon travail sur la phase post-florale en m'intéressant à la diversité de l'efficience de remplissage des grains et à la réponse aux changements climatiques (température, [CO_2]). Sur la base d'un raisonnement axé sur la régulation des puits, les objectifs principaux de de ce projet seront (i) d'identifier des marqueurs morphologiques et physiologiques du remplissage moteur d'un rendement plus élevé et (ii) de révéler des QTLs et gènes candidats contrôlant les caractères pertinents. Les hypothèses sous-jacentes de ce projet sont que (a) la force de puit est le moteur principal du rendement et (b) la régulation des puits est l'élément essentiel pilotant la force de puits (le taux d'épillets non remplis à maturité indique que la taille du puits n'est pas limitante). La régulation des puits le long de la panicule sera analysée en fonction de l'architecture de la panicule, et de signaux moléculaires impliqués dans la dynamique des sucres (T6P, éthylène) et de l'azote (strigolactones, glutamine). L'effet de la force et de la régulation des puits sur le compromis entre sénescence des feuilles de la tige et prélèvement post-floral de l'azote sera un axe marquant de ce projet dans l'optique d'augmenter le rendement (maintien de l'activité photosynthétique) et l'efficience d'utilisation de l'azote (prélèvement prolongé de l'azote du sol). La dominance apicale au sein de la panicule, très marquée chez le riz, peut être préjudiciable. La force de puits de la panicule pourrait être augmentée si davantage d'épillets se remplissaient simultanément. Des gènes candidats déjà répertoriés dans la littérature et des populations et des groupes de diversité pour les critères précités existent et seront mises à profit au sein de ce projet. Ces processus seront analysés en conditions distinctes de fertilisation azotée, de température et de [CO_2].